Canada

Fisheries and Oceans | Pêches et Océans

Canadian Journal of Fisheries and Aquatic Sciences

Journal canadien des sciences halieutiques et aquatiques

Government of Canada
Fisheries and Oceans

Scientific Information
and Publications Branch
Ottawa K1A 0E6

Gouvernement du Canada
Pêches et Océans

Direction de l'information
et des publications scientifiques
Ottawa K1A 0E6

The *Canadian Journal of Fisheries and Aquatic Sciences* has been published continuously since 1901, previously as *Contributions to Canadian Biology* 1901–25, *Contributions to Canadian Biology and Fisheries* 1926–34, *Journal of the Biological Board of Canada* 1934–37, and *Journal of the Fisheries Research Board of Canada* 1938–79.

Editorial policy

The *Journal* publishes original research articles and notes, critical reviews, Perspectives (essays of opinion or hypothesis), comments, and book reviews. Papers may concern cells, organisms, populations, ecosystems, or processes that affect aquatic production systems, and they should lead to identifiable conclusions or synthesis, which variously may amplify, modify, question, or redirect accumulated knowledge embodied in contemporary perceptions of a particular state of fisheries and aquatic sciences. They should demonstrate clearly a contribution to knowledge beyond the confirmatory state. Originality should relate to more than the particular (a certain year, place, taxon, or chemical compound) such that existing understanding is reformulated or extended.

It would assist the Editors if prospective authors identified briefly by covering letter (a) aspects of their papers that meet the foregoing objectives, (b) potential referees, and (c) other manuscripts contemplated or in press containing the same or similar information.

Submissions in English or French are acceptable. The information must be original, that is, not copyrighted, published, or submitted elsewhere except in abstract form or unless by written consent of the Editor. The *Journal* accepts no responsibility for statements made by contributors. The use of proprietary names does not imply endorsement of the product or company.

A charge is made for manuscripts published. When submitting a manuscript, an author must state that the charge will be accepted. See recent issues of the Journal for current page charges.

Guides

Guides for authors and typists appear in the first issue of each volume and are available free from the *Journal*.

Subscriptions

The *Journal* is issued monthly to form annual volumes of twelve numbers. Orders and inquiries regarding subscription rates must be sent directly to Supply and Services Canada, Ottawa, Ontario, Canada, K1A 0S9. Prepayment is required in Canadian funds to the order of "The Receiver General for Canada." Supplements to the *Journal* are issued periodically and must be purchased separately.

Microfilm

Issues from 1934 through the current volume can be purchased on 16- or 35-mm microfilm. Photocopies of individual articles or issues can be purchased from Xerox University Microfilms, 300 North Zeeb Road, Ann Arbor, Michigan 48106, USA.

Design: Ludvic Saleh & Associates, Ottawa

Conception graphique: Ludvic Saleh & Associates, Ottawa

Publié sans interruption depuis 1901, le *Journal canadien des sciences halieutiques et aquatiques* a paru sous plusieurs titres: *Contributions to Canadian Biology* 1901–25, *Contributions to Canadian Biology and Fisheries* 1926–34, *Journal of the Biological Board of Canada* 1934–37 et *Journal de l'office des recherches sur les pêcheries du Canada* 1938–79.

Politique de rédaction

Le *Journal* publie des articles et des notes fondés sur une recherche originale, des critiques, des essais portant sur une opinion ou une hypothèse (Perspectives), des commentaires et des comptes rendus de livres. Les textes peuvent avoir trait aux cellules, aux organismes, aux populations, aux écosystèmes ou aux processus qui influencent les systèmes de production aquatique. Ils doivent aboutir à des conclusions ou synthèses précises qui, de diverses façons, peuvent accroître, modifier, remettre en question ou réorienter le bagage actuel des connaissances et perceptions dans une discipline donnée des sciences aquatiques. Ils doivent clairement démontrer qu'ils contribuent aux connaissances en faisant plus que corroborer des faits. L'originalité doit dépasser le caractère particulier (une année, un endroit, un taxon ou un composé chimique donné) et tenir à une épuration ou à une reformulation des connaissances actuelles.

Les auteurs éventuels aideraient les rédacteurs s'ils identifiaient brièvement, dans une lettre d'accompagnement (a) les aspects de leurs textes qui répondent particulièrement aux objectifs indiqués ci-dessus, (b) des arbitres possibles et (c) d'autres manuscrits envisagés ou sous presse, dont la teneur est identique ou se rapproche de celui qui est soumis.

Les contributions peuvent être en anglais ou en français. Elles doivent être originales, c.-à-d. qu'elles ne doivent pas avoir fait l'objet d'un copyright, avoir été publiées ou soumises ailleurs, sauf sous forme abrégée ou avec le consentement du rédacteur. Le *Journal* décline toute responsabilité quant aux énoncés des contributeurs. L'utilisation des noms de marques de commerce ne signifie aucunement une sanction du produit en question ou de la compagnie qui le fabrique.

Les manuscrits acceptés sont sujets à des frais de publication. Quant un auteur présente un texte, il doit préciser que ces frais seront acceptés. On trouvera dans une récente livraison du *Journal* les taux par page en vigueur.

Guides

Le guide des auteurs et celui des secrétaires d'auteurs paraissent dans la première livraison de chaque volume et sont disponibles gratuitement du *Journal*.

Abonnement

Le *Journal* paraît tous les mois, formant ainsi un volume de douze numéros par année. On est prié d'adresser directement commandes et demande de renseignements relatifs à l'abonnement à Approvisionnements et Services Canada, Ottawa (Ontario), Canada K1A 0S9. Les paiements doivent être faits à l'avance en devises canadiennes, à l'ordre du « Receveur général du Canada ». Des Suppléments sont publiés périodiquement et doivent être achetés séparément.

Microfilms

On peut acheter sur microfilms de 16 ou 35 mm tous les numéros publiés depuis 1934. Des photocopies d'articles ou de numéros individuels sont aussi en vente auprès de Xerox University Microfilms, 300 North Zeeb Road, Ann Arbor, Michigan 48106, É.-U.

Canadian Journal of Fisheries and Aquatic Sciences

Journal canadien des sciences halieutiques et aquatiques

Volume 41, No. 2, February 1984

Volume 41, nº 2, février 1984

Scientific Information and Publications Branch/Direction de l'information et des publications scientifiques

J. Watson, Ph.D.	*Director and Editor-in-Chief/Directeur et rédacteur en chef*
Johanna M. Reinhart, M.Sc.	*Deputy Director and Editor/Sous-directrice et rédactrice*
D. G. Cook, Ph.D./Lorraine C. Smith, Ph.D.	*Assistant Editors/Rédacteurs adjoints*
J. Camp/G. J. Neville/P. M. Burke	*Publication Production/Productions des publications*
Y. Jean, Ph.D.	*French Abstracts/Résumés français*
R. O. Brinkhurst, Ph.D./J. R. M. Kelso, Ph.D.	*Book Review Editors/Rédacteurs des comptes rendus*

Editorial Board/Conseil de rédaction

P. J. Dillon	*Ontario Ministry of Natural Resources*
R. H. Green	*University of Western Ontario*
M. C. Healey	*Department of Fisheries and Oceans, Nanaimo*
S. R. Kerr	*Department of Fisheries and Oceans, Dartmouth*
P. H. LeBlond	*University of British Columbia*
L. Legendre	*Université Laval*
W. C. Leggett	*McGill University*
J. J. Magnuson	*University of Wisconsin*
M. Sinclair	*Department of Fisheries and Oceans, Halifax*
J. Sprague	*University of Guelph*
C. J. Walters	*University of British Columbia*
C. M. Wood	*McMaster University*

Editorial Office:
Scientific Information
and Publications Branch
Department of Fisheries and Oceans
Centennial Towers
200 Kent Street
Ottawa, Canada K1A 0E6

Bureau de rédaction :
Direction de l'information
et des publications scientifiques
Ministère des Pêches et des Océans
Les Tours Centennial
200, rue Kent
Ottawa, Canada K1A 0E6

Utilization of Phytoplankton by Zooplankton during the Spring Bloom in a Nova Scotia Inlet

R. J. Conover

Marine Ecology Laboratory, Bedford Institute of Oceanography, Dartmouth, N.S. B2Y 4A2

and P. Mayzaud

Biochimie Marine, Station Zoologique, 06230 Villefranche-sur-Mer, France

Conover, R. J., and P. Mayzaud. 1984. Utilization of phytoplankton by zooplankton during the spring bloom in a Nova Scotia inlet. Can. J. Fish. Aquat. Sci. 41: 232–244.

Coulter counter and microscope counts were used to estimate filtration and ingestion rates experimentally for total zooplankton caught by a 233-μm mesh net from two depths during the spring bloom in Bedford Basin. Initially, most phytoplankton were <20 μm with larger, chain-forming diatoms becoming more important as the bloom developed. Peak concentrations were >14 μg chlorophyll·L^{-1} and >1 mg C·L^{-1} and particle volume was >10 $mm^3 \cdot L^{-1}$. Maximum primary production was >30 mg C·$m^{-3} \cdot h^{-1}$. Dominant phytoplankton included *Chaetoceros septentrionale* early in the bloom, followed by *Skeletonema costatum* and *Thalassiosira*, *Rhizosolenia*, and *Chaetoceros* spp. Barnacle nauplii and *Acartia hudsonica* were the most common zooplankton near surface and *Pseudocalanus* sp. in deeper water. Ingestion was usually greatest at or near peaks in the Coulter counter particle spectrum. Filtration rate was proportional to grazer size and amount ingested and also to ambient particle concentration for near-surface but not deeper zooplankton. Higher ingestion was measured with the Coulter counter but microscopic counts gave higher filtration rates. Smaller surface-layer zooplankton apparently destroyed cells or chains that were not completely ingested. Microscopic estimates of particle volume ingested were 9–60% of that measured with the Coulter counter, suggesting utilization of detritus. Despite discrepancies in what the methods apparently measured, neither suggested a saturating functional response at ambient concentration, but with further concentration, both methods showed reduced filtration activity. Neither method revealed evidence for size-selective feeding, even when particles were compared on the basis of their maximum dimensions, but optical counts showed that single cells or chains of cylindrical shape were preferred to needle-like or spiney cells. Selection for biomass peaks could not be demonstrated using cell volume calculated from microscopic measurement. The 233-μm zooplankton utilized about 10–30% of daily primary production during the bloom.

On s'est servi d'un compteur Coulter et de comptages au microscope pour estimer expérimentalement les taux d'ingestion et de filtration du zooplancton total prélevé à deux profondeurs à l'aide d'un filet ayant un maillage de 233 μm, au cours de la floraison printanière dans le bassin de Bedford. Au début, la plus grande partie des organismes phytoplanctoniques avaient un diamètre inférieur à 20 μm, les chaînes de diatomées de plus grande taille devenant plus importantes avec la floraison. Les concentrations maximales ont été supérieures à 14 μg chlorophylle·L^{-1}, à 1 mg C·L^{-1} et à 10 $mm^3 \cdot L^{-1}$ pour le volume particulaire. Le niveau maximal de production primaire dépassait 30 mg C·$m^{-3} \cdot h^{-1}$. Les espèces dominantes de phytoplancton étaient *Chaetoceros septentrionale* au début de la floraison, suivie de *Skeletonema costatum* et *Thalassiosira*, puis de *Rhizosolenia* et *Chaetoceros*. Les nauplii de balane et *Acartia hudsonica* étaient les organismes zooplanctoniques les plus communs près de la surface et *Pseudocalanus* sp. en eaux plus profondes. Le taux d'ingestion était généralement le plus grand au niveau ou près des maximums dans le spectre particulaire du compteur Coulter. Le taux de filtration était proportionnel à la taille des consommateurs et à la ration ingérée, et aussi à la concentration particulaire du milieu pour le zooplancton près de la surface mais ce n'était pas le cas pour celui de plus grande profondeur. Un taux d'ingestion plus élevé a été mesuré avec le compteur Coulter, mais les comptages au microscope ont donné des taux de filtration plus élevés. Les petites espèces du zooplancton de surface ont semblé briser des cellules ou des chaînes qui n'étaient pas complètement ingérées. Les estimations au microscope du volume particulaire ingéré variaient entre 9 et 60% de celles mesurées par le compter Coulter, ce qui fait croire à l'utilisation de détritus. En dépit des différences entre ce que les deux méthodes ont semblé mesurer, aucune d'entre elles ne fait croire à une réponse fonctionnelle de saturation au niveau de la concentration particulaire du milieu, mais, avec une concentration plus forte, les deux méthodes ont montré une activité de filtration réduite. Aucune méthode n'a fait la preuve du choix des aliments selon leur taille même lorsque les particules étaient comparées d'après leurs dimensions maximales; cependant, les comptables optiques ont montré que les cellules seules ou les chaînes de cellules de forme cylindrique sont préférées aux cellules en forme d'épine ou d'épingle. L'ingestion préférentielle dans les pics de biomasse n'a pu être démontrée par le calcul du volume cellulaire à partir de mesures au microscope. Le zooplancton de 233 μm a utilisé entre 10 et 30% de la production primaire journalière pendant la floraison.

Received December 29, 1982
Accepted October 12, 1983

Reçu le 29 décembre 1982
Accepté le 12 octobre 1983

The response of filter-feeding crustaceans to increasing concentrations of food has given apparently conflicting results, depending at least in part on the design of the experiments. On the one hand, when copepods are given increasing amounts of laboratory-cultured phytoplankton over a short period of time, the ingestion rate initially increases until a nonlimiting concentration for each type of cell is reached, after which there is no further increase (McMahon and Rigler 1965; Frost 1972). In contrast, when zooplankton are fed natural particulate matter, the ambient concentration can sometimes be less than the critical concentration for saturation of the feeding response (Parsons et al. 1969), and over a period of many weeks, the ingestion rate in response to changes in probable food levels appears to be linear regardless of concentration (Poulet 1974; Reeve and Walter 1977; Conover 1978; Koeller et al. 1979). Mayzaud and Poulet (1978) have postulated that zooplankton in nature normally have time to acclimate their feeding response to changes in quantity and quality of their food supply, possibly through modification of the rate of synthesis or secretion of digestive enzymes. If time to acclimate is indeed the factor governing the response of zooplankton to variability in their supply of nourishment, then comparison of their ingestion rates and enzyme concentrations during a period of accelerating primary production, such as the spring bloom of boreal waters, should constitute a field test of the hypothesis. In Bedford Basin, N.S., the annual cycle of phytoplankton abundance includes a large peak in March and usually a somewhat smaller one in the September–October period. Concentrations of chlorophyll in excess of $10\,mg \cdot m^{-3}$ and production rates greater than $900\,mg\,C \cdot m^{-2} \cdot d^{-1}$ are common in the basin in mid-March (Platt 1975). This environment was chosen for intensive study during the spring of 1977. In this paper we consider the feeding behavior of the zooplankton community. The enzyme biochemistry of the zooplankton during this period is the subject of a companion paper (Mayzaud and Conover 1984).

Materials and Methods

Experimental animals and water were usually gathered from a regularly sampled station near the center of Bedford Basin, but on two occasions additional stations were included. For a description of this environment see Poulet (1973). Zooplankton were captured with a 0.75-m net of 233-μm mesh nylon bolting cloth rigged so that it could be opened and closed by a double release mechanism (General Oceanics Inc., Miami, FL). Horizontal tows were made near the area of maximum zooplankton concentration, generally in the upper 10 m, and also at a depth of about 30 m. The animals were immediately diluted with seawater from sampling depth previously taken with a 30-L Niskin bottle. Water from the same source was also used for grazing experiments, which were generally run in 1- or 3-L beakers using the stirring system described by Poulet (1973). On most occasions the ambient water was further concentrated by gentle filtration or diluted with filtered seawater to extend the range of concentration before grazing experiments were started. Normally the animals were selected at random from the stock population without regard to size or species, but care was taken to capture actively swimming individuals. On several occasions near the peak of the bloom, clogging of the plankton net resulted in capture of large numbers of nauplii and other young stages of representative zooplankton, and further separation into large-sized (B) and small-sized (E) populations with a somewhat coarser mesh netting (366 μm) was effected in the laboratory prior to selection of the individuals actually used in the grazing studies. The numbers selected varied considerably, ranging from about 100 to over 1000, and depended on a rather subjective estimate of average size of animals available and beaker size (Table 1). Other investigations (R. J. Conover, unpubl. data) suggested that there was no significant effect on grazing activity over the same range of concentration in 1-L beakers when all animals were from the same population.

Experimental beakers and control beakers without grazers were usually incubated for about 24 h at a temperature near that in the natural environment at depth of capture (Table 1). In reply to a recent criticism (Roman and Rublee 1980) of long incubations, we point out that our experimental temperatures were generally quite low (1–6°C) and that long incubations were necessary to get significant changes in particulate concentrations. We found no deterioration in the animals' performance when experiments were repeated following one or several days of further maintenance under the same laboratory conditions to which they were exposed before the initial experiments.

Samples were taken initially and at the end of the incubation period from both experimental and control beakers for Coulter counting (Coulter Electronics, Hialeah, FL), microscopic counts and measurement after preservation with Lugol's, and carbon and nitrogen analysis carried out with the Hewlett-Packard 185B Carbon Hydrogen Nitrogen Analyzer after filtration on 0.8-μm silver filters (Selas Flotronics, Spring House, PA). Following the grazing experiment the zooplankton were counted, identified, rinsed briefly in isotonic ammonium formate, and air dried in an oven at 70°C overnight. Dry weight and C–H–N content, also determined with the Hewlett-Packard 185B, were measured for animals from each experimental container.

Filtration rates were determined from changes in particle volumes, measured with the model T Coulter Counter®, and in microscopic cell counts, using the relation

$$(1)\quad F = \frac{v}{t} \ln \frac{P_0}{P_t}$$

where F is the filtering rate (millilitres) swept clear per unit time and per animal, v is the experimental volume (millilitres) per animal, t is time, and P_0 and P_t are the initial and final concentrations, respectively, of particles (cubic millilitres per litre or cells per litre). Because there were no systematic differences between initial and final controls and such changes as occurred were usually small, P_0 was taken as the final concentration in the control, in which case a correction for particle growth such as that used by Frost (1972) does not alter the value of F. Details of the Coulter counter grazing experiments are given in Table 1. Filtration rates were also calculated from net change in total particle concentration and from differences between control and experimental for specific channels, as an indicator of possible selective feeding behavior, and were compared with filtration rates calculated from changes in total cell numbers and in numbers of particular species.

Ingestion (I) in these experiments was determined as

$$(2)\quad I = \frac{v}{t}(P_0 - P_t)$$

and therefore should not be equated with the ingestion rate (R) calculated from the filtration rate as

$$(3)\quad R = F\bar{P}$$

TABLE 1. Background information on grazing experiments at ambient concentrations. E refers to total community of surface zone animals; B refers to coarse fraction of surface zone animals; D refers to animals from 30 m.

Date at start	Code	Experimental temperature (°C)	Experimental particle concentration ($mm^3 \cdot L^{-1}$)		Experimental volume (L)	Experimental time (h)	No. of animals	Mean dry weight per animal (μg)
			Initial	Control				
Feb. 8, 1977	E_1	1.1	0.640	0.831	0.86	24.1	273	14.5
	E_2	1.0				24.2	237	14.9
	E_3	1.2				24.2	276	15.2
	E_4	1.0				24.1	211	14.3
Feb. 28, 1977	E	1.1	3.870	3.535	1.96	24.0	1065	2.1
	B	1.3				24.7	440	4.5
	D	1.2				24.4	269	9.5
Mar. 2, 1977	E	1.0	4.487	4.341	2.06	24.2	781	2.6
	B	1.1				24.4	730	4.9
	D	1.1				24.6	409	9.3
Mar. 8, 1977	E	1.3	6.256	6.131	0.86	23.4	562	2.7
	B	1.4			0.86	23.4	341	5.9
	D	1.1			2.15	23.4	240	14.3
Mar. 10, 1977	E	1.2	7.878	8.947	2.15	23.6	428	2.9
	D	1.4			0.86	23.9	354	12.4
Mar. 15, 1977	E_{10}	1.6	7.940	8.153	0.86	23.3	410	2.7
	E_{15}	1.4				23.3	363	4.4
	D	1.5				23.4	432	9.3
Mar. 17, 1977	E	1.3	6.308	6.369	0.86	24.6	1039	2.8
	B_{15}	1.3			0.86		531	4.5
	B_{17}	1.2			0.86		299	4.6
	D	1.2			2.15		356	11.7
Mar. 21, 1977	E	1.3	6.866	7.167	0.86	23.1	383	4.5
	D	1.3				23.1	312	4.6
Mar. 25, 1977	E_1	1.5	8.618	7.932	0.86	47.6	146	4.1
	E_2	1.4					83	3.6
	D_1	1.3					146	11.7
	D_2	1.4					94	11.5
Mar. 29, 1977	E	2.4	6.607	5.577	2.10	23.3	292	3.0
	D	2.4				23.4	343	9.8
May 9, 1977	E_1	5.8	5.031	4.851	0.86	18.6	319	8.5
	E_2	6.0	4.670	4.489		18.7	429	10.0
	E_3	5.5	9.788	8.664			220	8.3
	E_4	5.3	3.681	3.053			212	8.7
	E_5	5.7	4.465	3.425			300	9.0

where $\bar{P}$ is the arithmetic or geometric mean particle concentration in the experimental container calculated from initial and final concentrations. If particle growth is positive in the control vessels, $I > R$ and if negative, $I < R$, but the differences are usually less than 10%. If one assumes that an individual grazer can have virtually no effect on its effectively infinite natural food environment and that F is a true constant, a better estimate of ingestion rate might be

$$R^* = FP_I \quad (4)$$

where P_i is the initial particle concentration. However, we use I instead of R or R^* because it describes the actual net changes in the container and thus is not affected by errors in determining F caused by alteration in chain length or by particle production from whatever source (Deason 1980) and facilitates the calculation of absorption (assimilation), which is determined as follows: if it is assumed that the ratio of carbon or nitrogen concentration to particle volume at t_0 defined as C_R or N_R, is fixed for the duration of the experiment, then the amount ingested is

$$I_C = \frac{v}{t}(P_0 \cdot C_R - P_t \cdot C_R) = \frac{vC_R}{t}(P_0 - P_t) \quad (5)$$

for carbon and

$$I_N = \frac{vN_R}{t}(P_0 - P_t) \quad (6)$$

for nitrogen, while the amounts absorbed for carbon and nitrogen are

$$A_C = \frac{v}{t}(C_0 - C_t)$$
$$A_N = \frac{v}{t}(N_0 - N_t) \quad (7)$$

with C_0 and N_0 and C_t and N_t being the initial and final concentrations of carbon and nitrogen in the particulate matter in the grazing beaker. We have examined C_R and N_R throughout the year in Bedford Basin and find a more or less constant relationship, but the weakly variability is too great to make a

general regression equation useful in application of equations 5 and 6. Hence, C_R and N_R were determined for each experiment. It is also necessary that C_t and N_t include all fecal carbon but no animals or parts of animals. Small errors in any of these measurements may lead to negative estimates or estimates of greater than 100% absorption, so that considerable care must be taken in subsampling; we recommend triplicate analyses, although this was not possible with 1-L experimental beakers.

Results

Description of the Spring Bloom

The spring bloom in Bedford Basin generally occurs in mid-March and is of relatively short duration, so we decided to begin our experiment the last week in February to provide a basal level for grazing measurements and enzyme concentration. As shown in Fig. 1 and 2, our timing was not perfect. By February 28, cell counts, particle volumes, particulate carbon and nitrogen, and chlorophyll concentrations revealed that the bloom was already well underway. For some parameters, data from at least one earlier date were available that suggested that the 1st wk of February should probably have been chosen as a baseline, but regrettably, zooplankton enzyme concentrations and phytoplankton cell counts were not determined prior to February 28. Reasons for the somewhat earlier bloom are not certain but meteorological information for Halifax showed that January 1977 was a bit cooler, dryer, and less windy and had considerably more hours of sunshine than monthly means averaged over the previous 109 yr (Environment Canada 1977). Increasing light and water column stability contribute to the onset of spring flowerings, which may be prolonged by pulses of enrichment associated with spring rains and high runoff (Sinclair et al. 1981).

Coulter counts and cell counts indicated a continuous succession of particle types and sizes. After the midwinter low when particle concentration was less than 1 $mm^3 L^{-1}$ (Fig. 3), production was initiated primarily by smaller forms such as the solitary diatom *Chaeotoceros septentrionale* (Fig. 4). As the bloom developed, the dominant peak of small-sized particles increased somewhat in size (Fig. 3) with the increasing importance of chain forming diatoms such as *Skeletonema costatum* and *Thalassiosira nordenskioldii* (Fig. 4). D. V. Subba Rao (Marine Ecology Laboratory, Bedford Institute of Oceanography, pers. comm.) also noted the initial dominance in Bedford Basin of nanoplankton (<20 μm), followed by a shift toward greater production by larger species. *Thalassiosira*, *Rhizosolenia*, and probably *Chaetoceros* spp. contributed to the increasing peak of large particles after March 8 (Table 2), and some of these formed chains of 10 or more cells.

Zooplankton Feeding

The general pattern of feeding at ambient particle levels as measured with the Coulter counter for the mixed zooplankton community did not differ greatly from that described by Poulet (1973, 1974) for *Pseudocalanus*. As shown in Fig. 5, grazing was usually highest in regions of the particle spectrum with the greatest concentration, regardless of size, or was displaced slightly to the right of the peaks, as observed by Wilson (1973). Comparison of shallow- and deep-water zooplankton fractions suggested that filtration rate was also more or less proportional to size of grazer (Table 1), but there were no differences in size selection. Nor was there any significant trend in filtration rate,

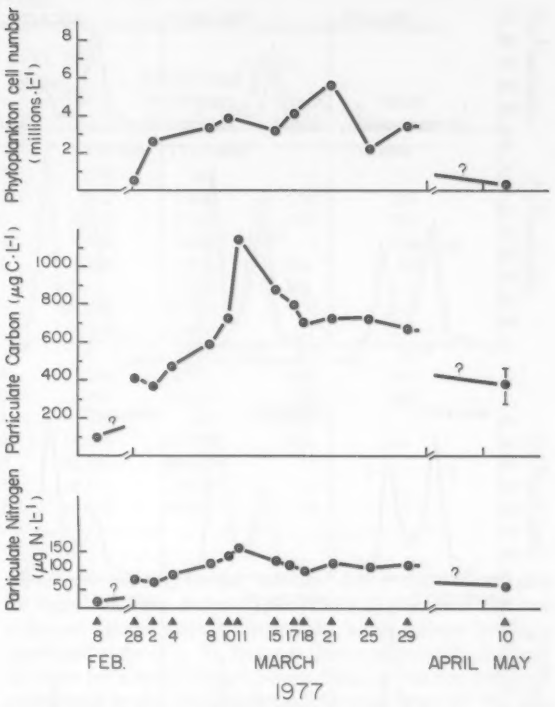

Phytoplankton cell number (millions·L⁻¹)
Particulate Carbon (μg C·L⁻¹)
Particulate Nitrogen (μg N·L⁻¹)
8 28 2 4 8 10 11 15 17 18 21 25 29 10
FEB. MARCH APRIL MAY
1977

FIG. 1. Changes in total phytoplankton cell numbers, particulate carbon, and particulate nitrogen at zooplankton sample depth in the euphotic zone during the spring bloom, 1977.

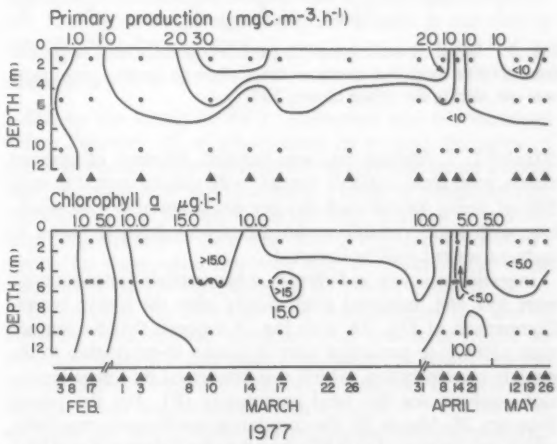


FIG. 2. Distribution of primary production over a 4-h incubation period determined by in situ ^{14}C incubation and of chlorophyll *a* measured by fluorescence during the spring bloom, 1977 (data provided by P. Lehman and D. V. Subba Rao).

corrected for size differences in the grazers, over the range of total ambient concentrations observed (Fig. 6).

By concentration and dilution of ambient samples, the total range of concentrations to which grazers were exposed was extended by about 20–49 times. When net change in particle volume was used as a criterion for calculation at highest concentrations of particles, which ranged from 18 to about

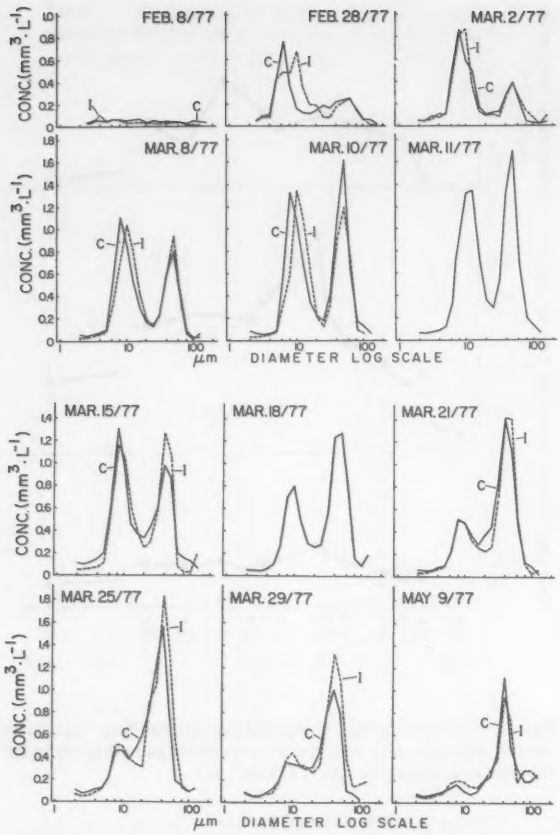


FIG. 3. Initial (I) and control (C) particle concentrations, or particle concentration from 5 m depth on dates when no grazing experiment was run, during the spring bloom, 1977.

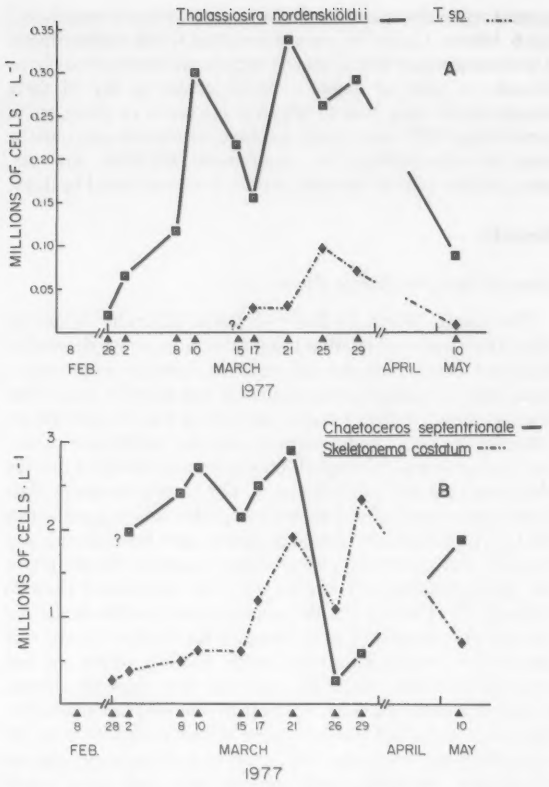


FIG. 4. Distribution of (A) *Thalassiosira* spp. and (B) *Chaetoceros septentrionale* and *Skeletonema costatum* during the spring bloom, 1977.

50 $mm^3 \cdot L^{-1}$, filtering rate was reduced. Dilution of ambient waters gave more variable results, with values from 0 to over 500 mL being filtered each day per milligram of dry zooplankton; with such variability, no differences from filtration in ambient water could be detected.

Ingestion was low in February when particle concentrations were low and increased dramatically after the bloom began. Comparison of Fig. 7A with Fig. 3 suggests that the surface zone animals in particular were ingesting in proportion to the particle concentration, which was confirmed by linear regression analysis for the total community (E). For the period February 28–March 29, the correlation coefficient r was 0.65, which was improved to 0.86 when data for February 8 and May 10 were included, although there was virtually no change in slope, being 0.18 initially and 0.17 when the information for the longer sampling period was added. If the larger fraction (B) was regressed separately the slope was not significant, but in this case there were only four data pairs to examine. The deepwater animals showed no significant response to concentration during the bloom period, but there were no measurements for this group when food concentrations were low.

As a check on the Coulter counter method of measuring filtration and ingestion by zooplankton, we also examined the phytoplankton community using microscopic counts; optical measurements of cell dimensions were used to compute cell volume. The proportion of detritus to recognizable cell types is probably lower during bloom periods, and the diatom-dominated spring forms are simpler in shape and thus easier to convert to volume using linear measurements than phytoplankton at other seasons, which should facilitate the comparison. Factors used to convert optical counts to the same units as Coulter counter volumes are given in Table 2, but note that the variability, especially for large cells, is high.

Ingestion rates, based either on Coulter counter volumes or on volumes calculated from cell counts, would appear to be in poor agreement (Fig. 7A and 7B). Over the first half of the experiment (February 28–March 17), cell count data yielded significantly lower estimates of ingestion based on a Wilcoxon matched-pairs signed-ranks test (Siegel 1956), while in the second half (March 17–March 29) the trend seemed to be reversed although this was not verifiable statistically. Even so, over the entire bloom period ingestion rates from Fig. 7B were significantly and positively correlated with concentration estimated from optical measurements for both the near-surface and subsurface zooplankton communities.

Similarly, there was poor agreement between filtration rates calculated from the two types of particle estimates and examined with the same nonparametric statistical method. In this case, cell counts gave generally higher estimates of filtration with the discrepancy being greater for the smaller, near-surface community than for the deeper *Pseudocalanus* group.

TABLE 2. Phytoplankton cell volumes (μm^3), chain length (numbers of cells), and average effective particle dimensions (μm) from Bedford Basin (1974 data from Taguchi and Platt 1978a).

Species	1977 volume range	Mar. 1–30, 1974, volume		Volume used in estimates of ingestion	Chain length	Mean dimensions
		Mean	SD			
Chaetoceros septentrionale	170–785	237	227	240	1	30
Chaetoceros affinis	565–3 534	1 401	172	1 400	<20	200
Chaetoceros sp.	4 241–25 133	8 705	5 112	8 700	<20	350
Nitzschia longissima	628–785	1 631	304	1 600	1	110
Nitzschia seriata	1 767–1 963	1 916	165	1 900	NA	50
Nitzschia sp.	—	—	—	2 000	NA	—
Rhizosolenia hebatata	78 540–94 248	30 933	29 819	31 000	1	—
Rhizosolenia setigera	—	10 881	3 752	11 000	1	—
Skeletonema costatum	226–785	—	—	320	13	55
Thalassiosira nordenskioldii	565–3 534	4 664	2 380	4 700	<20	150
Thalassiosira sp.	7 069–28 274	42 409	22 981	20 000	<20	260
Thalassionema nitzschioides	94–1 178	534	392	500	NA	—
Biddulphia aurita	—	20 920	14 626	21 000	NA	—
Peridinium sp.	—	17 740	20 264	18 000	1	—
Gyrodinium sp.	—	5 233	5 721	5 000	1	—
Dinophysis norvegica	—	24 443	14 656	25 000	1	—

Estimates of total volume usually showed a large discrepancy when automated and optical methods were compared. Agreement was good only on March 29 when optical methods showed maximum ingestion rates. On the remaining sampling dates direct cell counts accounted for between 9 and 60%, but usually less than 30%, of the Coulter counter volume. The nonevaluated material in optical counts probably represented detritus, inorganic particles, small, unrecognized cells, and microzooplankton.

Despite the apparent differences in what was being consumed and how much, as estimated by the two methods, the relationships between filtration rate and ambient food concentration were unaltered. Weight-specific filtration rate determined from total cell counts of unaltered water and plotted against total numbers of cells, or total particle volume calculated from microscopic counts, showed no significant positive or negative slope, just as shown for the Coulter counter data (Fig. 7). When ambient concentration levels were increased by up to 10 times through gentle back-filtration, cell counts also showed that feeding was reduced but filtering rates were still at least twice those determined with the Coulter counter. At concentrations less than ambient, mean filtration rates were greater than at ambient levels, but a few very high values increased the variance as well as the mean, making interpretation uncertain.

We also examined several aspects of size-selective feeding during the period February 28–March 29, using the microscopic data. Taking the *Pseudocalanus*-dominated deeper population because it showed the least time-related variability, we looked at the regressions between cell volume and filtration rate and between chain volume, based on an estimate of average cell number per chain (Table 2), and filtration rate; we found no slope in either case. Because many of the cells occurring in the spring plankton have spines or are irregular in shape and thus have effective dimensions, relative to a sieving device with fixed aperture size, considerably greater than their mean spherical diameter determined from Coulter counter volume, we also calculated a mean "diameter" based on average of maximum and minimum dimensions determined optically from spine tip to spine tip for the "average" cell or chain. Using data for eight dominant diatom types (Table 2), filtration rate was regressed against particle dimensions, again without finding a significant slope (Fig. 8). Nor was there a statistically discernible slope for a relationship between filtration and concentration contributed by the same eight particle types (Fig. 9). We then compared filtration rates (Table 3) for each of the eight dominant diatom complexes using a Kruskal–Wallis one-way analysis of variance (Siegel 1956). The means were clearly from more than one homogeneous population, suggesting that selective feeding, although apparently not related to cell size or concentration, had occurred.

Absorption

During the spring of 1977, absorption was not measured before February 28 or after March 29 so that the range of ambient concentration was relatively narrow and the mean quite high; nor was there any systematic change in weight-specific ingestion during this period (Fig. 7A). Perhaps it was not surprising that neither carbon nor nitrogen absorption showed a significant slope when regressed against concentration; mean values were 64.2% for carbon and 63.1% for nitrogen.

To examine the effect of food concentration and rate of ingestion on absorption efficiency over a broader range, we examined the 1977 data from experiments in which ambient concentrations were also diluted or concentrated. In this fashion the total range was increased from 4.6 $mm^3 \cdot L^{-1}$ (4.3–8.9) to 45.7 $mm^3 \cdot L^{-1}$ (1.1–46.8). Four regressions were computed for carbon absorption and four for nitrogen, two each related to concentration of potential food in the environment and two related to the actual amount of food ingested under parallel conditions (Table 4). All carbon regressions showed significant positive slope although the proportion of variance explained by the relationships was small and significance disappeared if two low absorption values, which might be questioned because of the potentially greater analytical errors associated with low concentration levels, were removed. None of the nitrogen regressions showed significant slope (Table 4).

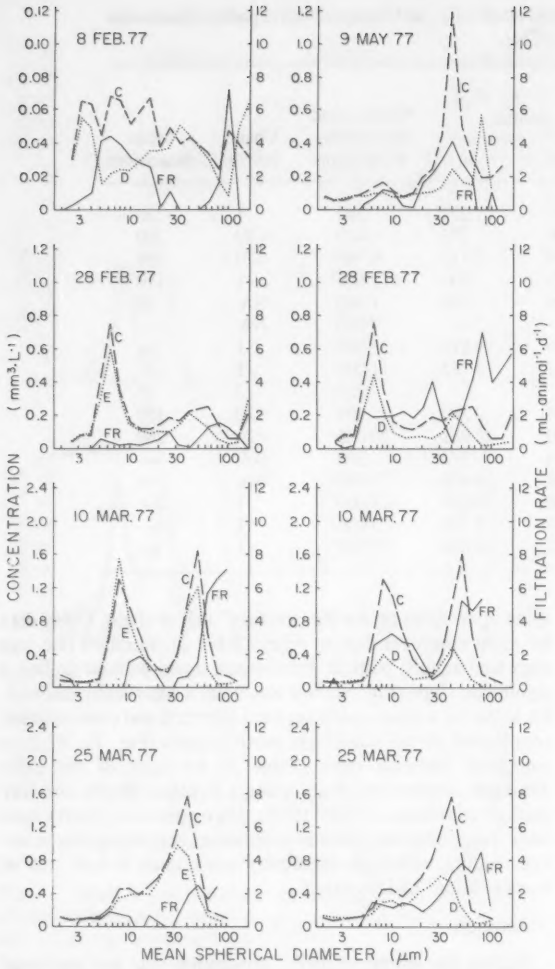


FIG. 5. Selected grazing experiments showing filtration rate (FR) and particle concentration in control (C) and experimental (E, euphotic zone animals; D, 30-m animals) bottles during the spring bloom, 1977.

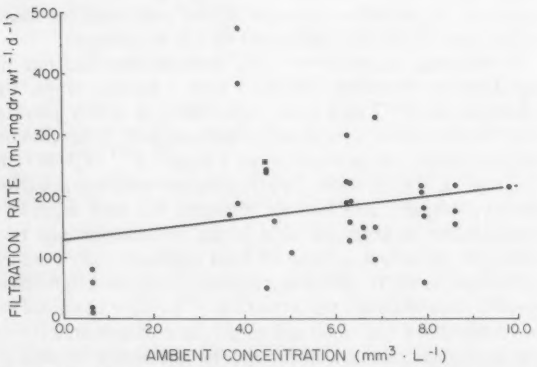


FIG. 6. Weight-corrected filtration rate plotted against ambient concentration during the spring bloom, 1977. The regression is not significant.

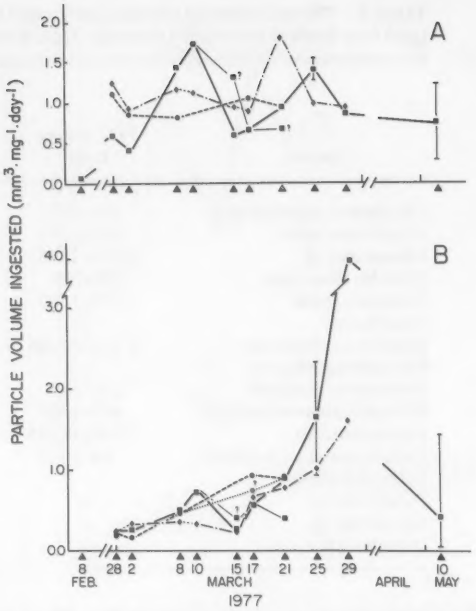


FIG. 7. (A) Weight-corrected ingestion determined from Coulter counter analysis of particle volume during the spring bloom, 1977. ■, total euthrophic zone animals; ●, large fraction of eutrophic zone animals; ◆, animals from 30-m depth; ?, experiment repeated with animals from same stock several days after capture. (B) Weight-corrected ingestion determined from optical counts and measured cell volumes during the spring bloom, 1977. Symbols as for Fig. 7A.

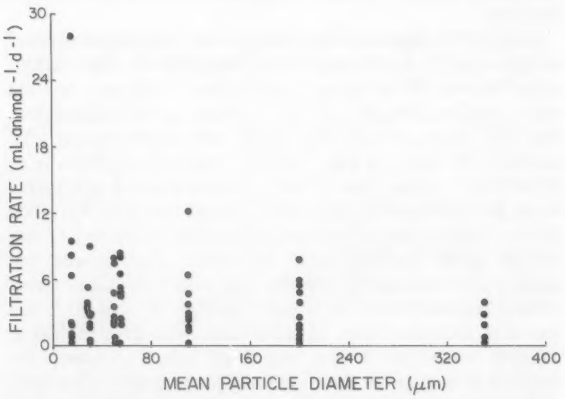


FIG. 8. Filtration rate for the deepwater zooplankton community plotted against the "average" dimensions from spine tip to spine tip for the "mean particle" size of eight cell types common during the spring bloom, 1977. The regression is not significant.

Discussion

Food Selection and Methods of Measuring Feeding

While it was not the original purpose of this paper to discuss methods used in studying aspects of zooplankton feeding biology, the recent appearance of several papers critical of certain of the techniques used here requires some comment. In the first of these papers chronologically, Deason (1980) has

TABLE 3. Average weight-specific filtration rate swept clear ($mL \cdot mg\ dry\ wt^{-1} \cdot d^{-1}$) for *Pseudocalanus*-dominated zooplankton feeding on eight different cell types, counted optically, as part of the natural particulate community occurring in Bedford Basin between February 28 and March 29, 1977. Kruskal-Wallis parameter $H = 430.9$ (df = 7) exceeds χ^2 at $P = 0.001$. Reject null hypothesis that all filtration rates are from a single population.

Species	No. of observations	Range of concentration of cells (thousands $\cdot L^{-1}$)	Filtration rate	
			Mean	SD
Chaetoceros septentrionale	9	374.0–4400.0	195.6	239.6
Chaetoceros affinis	10	3.4–105.0	337.1	210.9
Chaetoceros sp.	9	0.32–2.3	120.2	145.9
Nitzschia longissima	10	70.1–330.0	315.9	297.9
Nitzschia seriata	10	20.2–125.0	309.8	285.1
Skeletonema costatum	10	263.0–1770.0	464.6	274.5
Thalassiosira nordenskioldii	10	33.7–340.0	577.5	889.5
Thalassiosira sp.	5	30.0–125.0	425.6	168.9

TABLE 4. Regression equations relating the percentage absorption to concentration of food and amount ingested, spring bloom 1977 data. $*P \leq 0.05$, significant slope.

	Independent variables	N	Slope	Intercept	Coefficient of determination R^2
Carbon equations	Concentration ($\mu g\ C \cdot L^{-1}$)	43	0.006*	55.9	0.129
	Particle concentration ($mm^3 \cdot L^{-1}$)	43	0.473*	56.6	0.125
	Ingestion ($mm^3 \cdot mg\ dry\ wt^{-1} \cdot d^{-1}$)	30	11.10*	51.0	0.127
	Ingestion (% body $C \cdot d^{-1}$)	30	0.673*	47.6	0.165
Nitrogen equations	Concentration ($\mu g\ N \cdot L^{-1}$)	37	0.00008	60.4	0.000001
	Particle concentration ($mm^3 \cdot L^{-1}$)	37	0.036	59.8	0.0006
	Ingestion ($mm^3 \cdot mg\ dry\ wt^{-1} \cdot d^{-1}$)	30	−0.540	68.0	0.018
	Ingestion (% body $N \cdot d^{-1}$)	30	−0.416	69.5	0.023

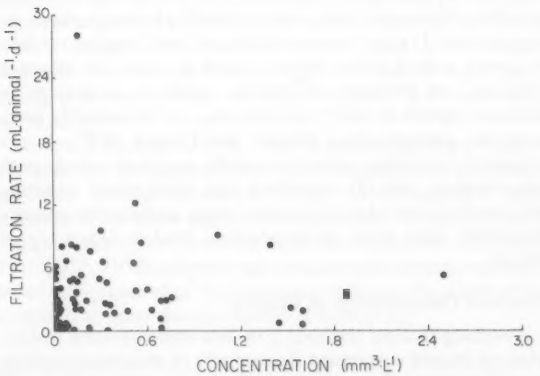


FIG. 9. Filtration rate for the deepwater zooplankton community plotted against cell volume contributed by each of the eight dominant cell types during the spring bloom, 1977. The regression is not significant.

shown how chain breakage and consequent particle production during feeding can affect the calculation of filtration rates and ingestion rates based on them (R, equation 3). While particle production was apparently not prominent in our experiments (Fig. 5), the amount produced for a channel must exceed the rate of utilization in the channel before it can be detected. To avoid this kind of error we prefer to use I (equation 2), based on net changes in particle volume, as our principal estimator of food uptake in Coulter counter experiments in which a variety of gazers and particle types interact.

Deason (1980) further demonstrated how the use of differences in apparent filtering rate in different parts of the particle spectrum as an index of selective feeding can give erroneous results. She also showed that the apparent tracking of biomass peaks or switching from one part of the spectrum to another could be artifacts of undetected chain breakage. It is therefore possible that any differences in resource utilization between surface-zone and deepwater zooplankton shown by filtration rate curves in Fig. 5 could lead to a false interpretation of selection processes, although they do demonstrate that different patterns in handling of particulate matter, whether through consumption or partial destruction, occurred. For example, apparently greater utilization of smaller sized particles by the larger deepwater zooplankton during the February 28 experiment may well reflect greater small-particle production by smaller surface-zone animals feeding on larger cells. Indeed, net particle production was observed on March 10 for surface-zone grazers. Cell count data suggested that *Skeletonema* and *Thalassiosira* were removed equally readily by both near-surface E and deeper D animals, but surface plankton tended to consume more *Chaetoceros* spp., and deep animals more *Nitzschia* spp. Spines of *Chaetoceros* and large *Thalassiosira*

would be more difficult to ingest by smaller animals without producing some debris.

In the second of these recent papers critical of certain grazing methods, Harbison and McAlister (1980) drew attention to the potential differences between particle size, described from its electrical resistance as an equivalent spherical diameter, and the true linear dimensions of a cell or colony of cells. They also found some differences in apparent volume of cells measured optically and with the Coulter counter, the discrepancy being greatest when a large clone of the fusiform diatom *Rhizosolenia setigera* was tested. However, our own observations using cells of cylindrical shape with similar length to width ratios ranging from a few to over 300 μm in diameter and using Coulter counter apertures from 70 to 1000 μm in diameter showed good agreement between calculated and electronically measured volume.

Variability in volume estimation for red blood cells in the Coulter counter system has been recognized for some time and was examined with a scale model by Thom et al. (1969). Edge and shape effects tend to skew the distribution of erythrocytes but do not greatly effect the measurement of their total volume (Merrill et al. 1971; Kubitschek 1971). Johnson (1974), also using a scale model of a multiple-electrode zooplankton counter (Boyd and Johnson 1969), found that apparent volume of a particle might be over- or under-estimated depending on its shape, orientation during transit, and position on the diameter of the orifice, yielding potential errors in measuring volume of up to 35%. However, we question the validity of extrapolation from a system with a scale exaggeration of 7.6×10^4 (or 10^3 in Thom et al. 1969) because viscous forces are much more important in the vicinity of a small aperture. Even so, the accumulated sum of positive and negative errors should approach zero; thus, the total concentration of natural seston measured with the Coulter counter should not be seriously in error, although some flattening of the spectral topography might take place.

In any event, our data show clearly that microscopic methods and the Coulter counter gave different estimates of particle concentration, filtration rate, and ingestion (Fig. 7); usually, optical methods yielded higher filtration rates and lower ingestion rates. Moreover, the discrepancy was usually greatest when the average grazer was small and perhaps became even more exaggerated as the mean particle size increased toward the end of the bloom. The number of cells destroyed or damaged without being completely ingested increases with cell size and abundance (Conover 1966; Peruyeva 1971) and surely, smaller grazers will be less successful feeding on large particles than large grazers. Cellular debris from such destructive feeding would probably be overlooked by the microscopic counter but recorded by the electronic device. Agreement between optical and electronic estimates of seston concentrations was also better when particles averaged larger, and probably when the majority were easily identified, geometrically simple shapes. We would argue then that the Coulter counter gives a more accurate picture of material actually consumed and would question the usefulness of a filtration rate, as determined from changes in cell numbers, to calculate ingestion rate, except possibly with certain laboratory cultures, the cells of which are known to be ingested whole by the grazer. If we define "filtration rate" as the "volume swept clear" per unit time, particle removal as determined by an electronic gating-type counter appear to be a better criterion than chain or cell "disappearance" on which to calculate a useful rate. Whether or not one accepts our argument about the merits of estimates of grazing based on changes in particle concentration, there is no evidence from comparison with the cell count data that the general relationships between filtration rate and particle concentration are altered.

Based on volumes calculated from cell counts we could find no evidence that the zooplankton fed selectively on biomass peaks by increasing their filtration rate on specific particles as they became more abundant (Fig. 9), which generally supports the arguments of Deason (1980) that earlier observation of such behavior by Poulet (1973) and others could be artifacts. Higher ingestion rates at concentration peaks are a consequence of constant filtration and need not indicate selection. Nor could we find a relationship between grazing and particle size, whether based on equivalent spherical diameter or on average dimensions of cells or chains including spines, thus contradicting most theories of size-selective feeding. Our visual observations of the utilization of eight phytoplankton types, as part of a natural particle assemblage, suggest that spiney or needle-like cells such as *Chaetoceros* spp. or *Nitzschia longissima*, which should be readily retained on a conventional netting, were less favored by some zooplankton than simple chain forms with cylindrical cells, in agreement with a number of other observations including recent ones by Kukina (1976) and Gruzov and Voloshina (1977). We grant that the interpretation of selective feeding using an electronic sensing zone device may require application of some different methods of calibration and suggest that it is frequently possible to determine the particle type contributing to a spectral peak by selective screening with examination of the material retained or that missing from the screened sample. Fortunately, those cell types most difficult to measure accurately with optical methods because of their irregular projections or spines are those most readily retained by screens. Such methods were used to determine the dominant cell types in experiments reported by Conover (1978) showing selection against dinoflagellates of the genus *Ceratium*.

Even though the Coulter counter and microscopically generated data do not agree completely, we think the following generalizations concerning selective feeding by zooplankton are supportable: (1) at low concentrations of food, feeding tends to be spread over a wider range of particle sizes, (2) although "tracking" or selection of biomass peaks as a strategy to facilitate capture of raidly reproducing, and presumably more nutritious phytoplankton (Poulet and Chanut 1975), is not supported, maximum ingestion usually occurs at or near peak concentration, and (3) everything else being equal, meaning also that the particle has a "suitable" shape and is not chemically distasteful, only then do zooplankton tend to select bigger objects.

Effects of Concentration on Feeding

Assuming that our methods give data approximating reality, what can be said concerning the response of mixed zooplankton to an increasing food supply taking place over a period of several weeks? Those from the upper waters where the phytoplankton was most abundant responded by increasing their ration in proportion to food available. Filtration rates remained constant or perhaps increased slightly. Over the entire year, Bedford Basin zooplankton show a significant positive regression between filtration rate and food supply (Conover and Huntley 1980). However, filtration rates were almost always depressed when their natural food levels were further concentrated and offered to the zooplankton without previous conditioning.

Although it is well established that zooplankton feeding tends toward saturation with increasing food availability, the functional response has not been adequately described. Suschenya (1962) may have been the first to fit a negatively accelerating exponential function to ingestion data for a zooplankton animal, and Parsons et al. (1967) modified this kind of relationship to include a lower concentration threshold sometimes necessary to initiate a feeding response. Frost (1972) used two straight lines to fit grazing rates for *Calanus pacificus* to changes in abundance of diatoms and showed that satiation concentration varied with cell size in such a way that maximum ration was approximately the same. Later, when Mullin et al. (1975) reexamined Frost's (1972) data, they could find no statistically valid reason for preferring any of three different models, either the rectilinear of Frost (1972), the quasi-hyperbolic of Parsons et al. (1967), or a Michaelis–Menton, adapted from enzyme kinetics. The rectilinear curves passed through the origin, suggesting a constant filtration rate down to zero food, while the curvilinear relationships intercepted the abscissa at concentrations greater than those frequently observed off southern California where *C. pacificus* abounds. The behavior of any of these models at low food concentrations is inconsistent with our data from Bedford Basin and would appear to be energetically inefficient as well.

The significance of a lower initiating threshold and factors determining its level have been relatively contentious issues. The importance of a lower threshold, serving as a refugium for prey species, adds stability to some ecosystem models (Steele 1974; Murdoch and Oaten 1975), but the initiating concentration for zooplankton appears to be quite variable and perhaps related to particle size (Frost 1975; Conover 1978). While Frost (1975) observed a reduction in filtering rate when ingestion fell below 15% of the maximum hourly rate of *C. pacificus*, there was no absolute cutoff as suggested in most previous models.

Earlier, Holling (1959) classified the rectilinear and negatively accelerating types of functional responses as types 1 and 2, respectively, and concluded from work with small mammals that the response could also assume a sigmoid form (type 3), where the finding of a few prey items, reinforced by learning, triggered an initially accelerating feeding behavior. In a later model, Holling (1965) classified types 1 and 2 as invertebrate responses with the type 3 being largely confined to vertebrates, which presumably have a higher capacity for associative behavior.

Although Holling (1959, 1965) found ample experimental evidence for the sigmoid functional response, his computer-generated simulation model of the system required large numbers of variables and lacked generality. It was not made clear how type 2 and 3 curves might be interrelated. Recently, Real (1977, 1979) adapted traditional enzyme kinetic modeling to the interpretation of the functional response for a vertebrate system. The generalized equation is written as

$$(8)\quad f = \frac{kA^n}{\chi + A^n}$$

where f is the feeding rate, k is the saturation or maximum feeding rate, A is food concentration, χ is food concentration that generates half-maximum feeding, clearly analagous with the half-saturation constant in the Michaelis–Menton equation, and n is a parameter that relates the acceleration in food detection to food increase; in one line of reasoning, n might be related to the "intelligence" of the predator. When $n = 1$ equation 8 assumes the Michaelis–Menton (type 2) form, but if $n > 1$ the curve becomes sigmoidal (type 3).

To the present, a type 3 response for organisms other than vertebrates appears to have been considered only for invertebrate predators and parisitoids by Hassell et al. (1977) even though the optimal foraging model developed by Lehman (1976) for a non-selective filter feeder can also generate a sigmoid functional response. Seale (1982), while working with a vertebrate suspension feeder, also recognized that the broad taxonomic categorization of functional response and feeding type is too restrictive. For marine zooplankton, the accumulated evidence, particularly with respect to the form of the lower initiating threshold, clearly does not universally favor the use of a hyperbolic or negative exponential model. Our seasonal studies of zooplankton behavior suggest that the form of the response is highly variable and hardly attributable to learning processes in the usual vertebrate sense. Rather, the explanation might be associated with adaptive responses of enzymes to substrates in a variable environment. If so, the kinetics that Real (1977) so elegantly adapted to the vertebrate behavior pattern might also be extended for interpretation of invertebrate responses.

While a number of monomeric enzymes react according to Michaelis–Menton kinetics and produce type 2 responses to increasing substrate, oligomeric enzymes, which are made up of multiple reactive subunits, can show "cooperativity" wherein the initial contact between substrate and reactive site predisposes the molecule to react with more substrate. Thus, the binding process is initially accelerated but then deaccelerates as the available sites become utilized.

We make this analogy not because we believe that the kinetics of a single oligomeric enzyme necessarily control the functional response of a zooplankton animal, but rather we wish to emphasize that other mechanisms exist by which a type 3 response can occur without evoking sophisticated behavior. Any kind of a feedback mechanism, regardless of the kind of information being transmitted, that results in enhancement of the initiating process should produce a type 3 response.

Zooplankton–Phytoplankton Interactions during the Bloom

In the spring of 1977 we did not make routine quantitative plankton tows; however, there are detailed analyses for the same season from 1971 and 1972 (S. A. Poulet and R. J. Conover, unpubl. data). A mean population density for those years from the same mesh net (233 μm) that we used to capture our experimental animals was 12 480 animals·m^{-3} (14 dates, SD = 2527) between mid-February and early April 1971 and 12 120 animals·m^{-3} (6 dates, SD = 1359) in 1972. In subsequent calculations it was assumed that 12 000 zooplankters·m^{-3} were functioning at the rates that we measured during the spring of 1977, although if younger copepodids, nauplii, and other microzooplankton taken with a 75-μm mesh net were included the total population could be up to 10 times more numerous based on 1971–72 information. We have also assumed that these animals were distributed uniformly over a 30-m water column, which is an approximate average for the environment calculated from data given in Platt and Conover (1971). To calculate the community carbon budget shown in Table 5, we further assumed that the weighted mean zooplankton size calculated for our experimental animals (from Table 2) was the true mean size on a particular date. Standing crop of carbon was estimated from Fig. 1 assuming that the distribution was

TABLE 5. Carbon balance for the pelagic community of Bedford Basin, spring bloom 1977, based on a 30-m water column. K_1, gross; K_2, net; Neg., negative.

Sample dates	Standing crop of particulate carbon ($g\,C \cdot m^{-2}$)	Primary production ($g\,C \cdot m^{-2} \cdot d^{-1}$)	Zooplankton ingestion ($g\,C \cdot m^{-2} \cdot d^{-1}$)	Primary production grazed (%)	Respiratory requirement ($g\,C \cdot m^{-2} \cdot d^{-1}$)	Growth efficiency (%)	
						K_1	K_2
Feb. 8	2.8	0.08	0.036	45	0.137	Neg.	Neg.
Feb. 28	12.4	0.61	0.112	18	0.066	1.1	1.8
Mar. 2	10.9	0.98	0.142	14	0.085	Neg.	Neg.
Mar. 8	17.4	1.69	0.216	12	0.095	16.0	26.7
Mar. 10	21.7	1.69	0.308	18	0.102	26.9	44.8
Mar. 15	26.2	2.06	0.374	18	0.103	32.5	54.1
Mar. 17	23.7	1.32	0.178	23	0.087	11.1	18.5
Mar. 21	21.7	1.15	0.189	16	0.084	15.6	25.9
Mar. 25	21.6	1.06	0.311	29	0.107	25.6	42.7
Mar. 29	20.1	0.77	0.250	32	0.107	17.2	28.7
May 10	13.1	1.42	0.183	13	0.154	Neg.	Neg.

uniform over the upper 20 m and that an average concentration of 140 $mg \cdot m^{-3}$ occurred at 30 m throughout the period based on observations by Taguchi and Platt (1978b) for the spring of 1974. Hourly primary production estimates in Fig. 2, based on 4-h incubations over the period of maximum light intensity, were integrated over depth assuming a compensation depth at 15 m, corrected to daily production using the 4-h energy fractions for nearby St. Margaret's Bay given in Platt and Irwin (1968), and finally linearly interpolated between dates, where necessary to coincide with dates of the grazing experiments (Table 5). Ingestion rates (cubic millimetres per animal per day) were converted to carbon ingested using the appropriate carbon to particle volume ratio for the date, standardized to percentage of carbon weight ingested for each size class of grazer, and averaged before being multiplied by the population density, always 3.5×10^5 animals in a 30-m water column. Respiratory requirements were calculated for the average-sized zooplankton on each date, assuming a respiratory coefficient of 0.8, from an equation given in Conover and Mayzaud (1976) relating respiration to temperature and size for Bedford Basin zooplankton. To calculate growth efficiency we first assumed assimilation to be 60% of ingestion, which is about the average value for these experiments obtained with any of the equations in Table 4. Growth was then assumed to be the difference between carbon assimilated and that respired, considering the amount of organic carbon excreted to be negligible. Gross growth efficiency (K_1, percent) is then carbon of growth over carbon ingested ($\times 100$), while net growth efficiency (K_2) is growth over carbon assimilated ($\times 100$).

Within the limits of available data the carbon budget looks about right. Between roughly 10 and 30% of the daily primary production during the spring bloom was probably consumed by the mesozooplankton grazers (Table 5). The microzooplankton community, which consists largely of crustacean developmental stages during this season, might have consumed as much again of the recently produced carbon (Beers and Stewart 1971; Capriulo and Carpenter 1980). Nonetheless, a significant fraction of the total spring production would probably not be consumed in the water column, some being exported with the net offshore exchange but the majority sinking to the bottom, thus accounting for the increase in chlorophyll in sediment trap samples following winter–spring blooms, which was observed in the same environment by Hargrave and Taguchi (1978). Smetacek et al. (1978) observed a similar phenomenon in the Bornholm Basin of the Baltic Sea with about the same time lag, 2–3 wk, before the bloom phytoplankton appeared in sediment traps. Both groups of authors attributed the inbalance between primary production and consumption during this season to low populations of overwintering zooplankton. In Bedford Basin, late summer mesozooplankton samples (233-μm net) are indeed an order of magnitude more abundant than spring ones (S.A. Poulet and R. J. Conover, unpubl. data). Predation by chaetognaths and hydromedusae probably keep spring zooplankton populations from responding rapidly to the phytoplankton increase (Conover and Mayzaud 1976).

There is good agreement among the several estimates of grazing impact on primary production for boreal neritic zooplankton communities of the *Pseudocalanus–Acartia* type. Riley (1956) estimated that 26% of the primary production of Long Island Sound went to the mesozooplankton on a yearly basis, but only about 10% of the spring flowering was utilized. A similar level of consumption by zooplankton was estimated by Skjoldal and Lännergren (1978) in the later part of the spring bloom in a Norwegian fjord, and they noted grazing removal of around 0.1 $g\,C \cdot m^{-2} \cdot d^{-1}$ in the post bloom period, again in fair agreement with our observations (Table 5). Zooplankton grazing accounted for 5–6.2% of primary production during the spring bloom in the Bering Sea at the landward end of the section, 15–86.6% in the midshelf region, and 15–29.4% further offshore (Dagg et al. 1982). Ecological efficiencies (secondary production/primary production) considerably less than 1% were observed during the spring bloom in Akkeshi Bay, Japan, by Taguchi and Fukuchi (1975). In Narragansett Bay, RI, the mean filtration rate for the spring period was 295 $mL \cdot mg\ dry\ wt^{-1} \cdot d^{-1}$ (Martin 1970), while in somewhat colder Bedford Basin it was 196 with a standard deviation of 86 for 32 observations from late February to early May. Respiratory and grazing rates for the smaller copepods in Saanich Inlet, B.C., in winter given by Koeller et al. (1979) were of a similar range to those for Bedford Basin, except that their estimate of the amount of carbon ingested was substantially higher, apparently because their factor for converting Coulter counter

volume to carbon was considerably greater than ours. Considering the wide geographic separation, differences in analytical methods, diversity of species (although most belong to common genera), and the considerable differences in temperatures among these several sets of observations the similarity in their output is reassuring.

Acknowledgments

We are grateful to M. Paranjape for his assistance in the field and laboratory, M. Huntley for making the phytoplankton counts, and P. Lehman and D. V. Subba Rao for correlative data gathered from Bedford Basin during the period of our study. D. V. Subba Rao also identified some of the phytoplankton. This work was partially supported by NATO grant No. 1401.

References

BEERS, J. R., AND G. L. STEWART. 1971. Micro-zooplankton in the plankton communities of the upper waters of the eastern tropical Pacific. Deep-Sea Res. 18: 861–883.

BOYD, C. M., AND G. W. JOHNSON. 1969. Studying zooplankton populations with an electronic zooplankton counting device and the LINC-8 computer, p. 83–90. *In* J. D. Mudie and C. B. Jackson [ed.] Applications of sea going computers. Marine Technology Society, Washington, DC.

CAPRIULO, G. M., AND E. J. CARPENTER. 1980. Grazing by 35 to 202 μm microzooplankton in Long Island Sound. Mar. Biol. 56: 319–326.

CONOVER, R. J. 1966. Feeding on large particles by *Calanus hyperboreus* (Kröyer), p. 187–194. *In* H. Barnes [ed.] Some contemporary studies in marine science. Allen and Unwin, London.

1978. Feeding interactions in the pelagic zone. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 173: 66–76.

CONOVER, R. J., AND M. E. HUNTLEY. 1980. General rules of grazing in pelagic ecosystems, p. 461–485. *In* P. G. Falkowski [ed.] Primary productivity in the sea. Plenum, New York and London.

CONOVER, R. J., AND P. MAYZAUD. 1976. Respiration and nitrogen excretion of neritic zooplankton in relation to potential food supply. 10th European Symposium on Marine Biology, Ostend, Belgium, Sept. 17–23, 1975. Vol. 2: 151–163.

DAGG, M. J., J. VIDAL, T. E. WHITLEDGE, R. L. IVERSON, AND J. J. GOERING. 1982. The feeding, respiration, and excretion of zooplankton in the Bering Sea during the spring bloom. Deep-Sea Res. 29A: 45–63.

DEASON, E. E. 1980. Potential effect of phytoplankton colony breakage on the calculation of zooplankton filtration rates. Mar. Biol. 57: 279–286.

ENVIRONMENT CANADA ATMOSPHERIC ENVIRONMENT. 1977. Monthly meteorological summary, March 1977. Environment Canada, Ottawa, Ont.

FROST, B. W. 1972. Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod *Calanus pacificus*. Limnol. Oceanogr. 17: 805–815.

1975. A threshold feeding behavior in *Calanus pacificus*. Limnol. Oceanogr. 20: 263–266.

GRUZOV, L. N., AND G. V. VOLOSHINA. 1977. On the mechanism regulating food consumption in marine copepods. Oceanology 16: 498–502.

HARBISON, G. R., AND V. L. MCALISTER. 1980. Fact and artifact in copepod feeding experiments. Limnol. Oceanogr. 25: 971–981.

HARGRAVE, B. T., AND S. TAGUCHI, 1978. Origin of deposited material sedimented in a marine bay. J. Fish. Res. Board Can. 35: 1604–1613.

HASSELL, M. P., H. H. LAWTON, AND J. R. BEDDINGTON. 1977. Sigmoid functional responses by invertebrate predators and parasitoids. J. Anim. Ecol. 46: 249–262.

HOLLING, C. S. 1959. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. Can. Entomol. 91: 293–320.

1965. The functional response of predators to prey density and its role in mimicry and population regulation. Mem. Entomol. Soc. Can. No. 45: 3–60.

JOHNSON, G. W. 1974. On measuring zooplankton *in situ* using the resistive pulse technique. Ph.D. thesis, Dalhousie University, Halifax, N.S.

KOELLER, P. A., J. E. BARWELL-CLARKE, F. WHITNEY, AND M. TAKAHASHI. 1979. Winter conditions of marine plankton populations in Saanich Inlet, B.C. Canada. III. Meso-zooplankton. J. Exp. Mar. Biol. Ecol. 37: 161–174.

KUBITSCHEK, H. E. 1971. Distortion in Coulter Counters and the applicability of the Collins–Richmond principle. Biophys. J. 11: 124–126.

KUKINA, I. V. 1976. Experimental study of the consumption of algae of different sizes by marine copepods. Oceanology 15: 355–358.

LEHMAN J. T. 1976. The filter-feeder as an optimal forager, and the predicted shapes of feeding curves. Limnol. Oceanogr. 21: 501–516.

MARTIN, J. H. 1970. Phytoplankton–zooplankton relationships in Narragansett Bay. IV. The seasonal importance of grazing. Limnol. Oceanogr. 15: 413–418.

MAYZAUD, P., AND R. J. CONOVER. 1984. Distribution of digestive enzymes in the zooplankton during the spring bloom in a Nova Scotia inlet. Can. J. Fish. Aquat. Sci. 41: 0000–0000.

MAYZAUD, P., AND S. A. POULET. 1978. The importance of the time factor in the response of zooplankton to varying concentrations of naturally occurring particulate matter. Limnol. Oceanogr. 23: 1144–1154.

MCMAHON, J. W., AND F. H. RIGLER. 1965. Feeding rate of *Daphnia magna* Straus in different foods labelled with radioactive phosphorus. Limnol. Oceanogr. 10: 105–113.

MERRILL, J. T., N. VEIZADES, H. R. HULETT, P. L. WOLF, AND L. A. HERZENBERG. 1971. An improved cell volume analyzer. Rev. Sci. Instrum. 42: 1157–1163.

MULLIN, M. M., E. F. STEWART, AND F. J. FUGLISTER. 1975. Ingestion by planktonic grazers as a function of concentration of food. Limnol. Oceanogr. 20: 259–262.

MURDOCH, W. W., AND A. OATEN. 1975. Predation and population stability. Adv. Ecol. Res. 9: 1–131.

PARSONS, T. R., R. J. LEBRASSEUR, AND J. D. FULTON. 1967. Some observations on the dependence of zooplankton grazing on the cell size and concentration of phytoplankton blooms. J. Oceanogr. Soc. Jpn. 23: 10–17.

PARSONS, T. R., R. J. LEBRASSEUR, J. D. FULTON, AND O. D. KENNEDY. 1969. Production studies in the Strait of Georgia. Part II. Secondary production under the Fraser River plume, February to May, 1967. J. Exp. Mar. Biol. Ecol. 3: 39–50.

PERUYEVA, YE. G. 1971. Certain aspects of the feeding behaviour of *Calanus helgolandicus* and *C. glacialis* in experiments. VNIRO 87: 121–128. (Fish. Res. Board Can. Trans. Ser. No. 2603)

PLATT, T. 1975. Analysis of the importance of spatial and temporal heterogeneity in the estimation of annual production by phytoplankton in a small, enriched, marine basin. J. Exp. Mar. Biol. Ecol. 18: 99–109.

PLATT, T., AND R. J. CONOVER. 1971. Variability and its effect on the 24 h chlorophyll budget of a small marine basin. Mar. Biol. 10: 52–65.

PLATT, T., AND B. IRWIN. 1968. Primary productivity measurements in St. Margaret's Bay, 1967. Fish. Res. Board Can. Tech. Rep. No. 77: 123 p.

POULET, S. A. 1973. Grazing of *Pseudocalanus minutus* on naturally occurring particulate matter. Limnol. Oceanogr. 18: 564–573.

1974. Seasonal grazing of *Pseudocalanus minutus* on particles. Mar. Biol. 25: 109–123.

POULET, S. A., AND J. P. CHANUT. 1975. Non-selective feeding of *Pseudocalanus minutus*. J. Fish. Res. Board Can. 32: 706–713.

REAL, L. A. 1977. The kinetics of functional response. Am. Nat. 111: 289–300.

1979. Ecological determinants of functional response. Ecology 60: 481–485.

REEVE, M. R., AND M. A. WALTER. 1977. Observations on the existence of lower threshold and upper critical food concentrations for the copepod *Acartia tonsa* Dana. J. Exp. Mar. Biol. Ecol. 29: 211–221.

RILEY, G. A. 1956. Oceanography of Long Island Sound, 1952–1954. IX. Production and utilization of organic matter. Bull. Bingham Oceanogr. Collect. Yale Univ. 15: 324–344.

ROMAN, M. R., AND P. A. RUBLEE. 1980. Containment effects in copepod grazing experiments: a plea to end the black box approach. Limnol. Oceanogr. 25: 982–990.

SEALE, D. B. 1982. Obligate and facultative suspension feeding in anuran larvae: feeding regulation in *Xenopus* and *Rana*. Biol. Bull. 162: 214–231.

SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York, Toronto, London.

SINCLAIR, M., D. V. SUBBA RAO, AND R. COUTURE. 1981. Phytoplankton temporal distributions in estuaries. Oceanol. Acta 4: 239–246.

SKJOLDAL, H. R., AND C. LÄNNERGREN. 1978. The spring phytoplankton bloom in Lindaspollene, a land-locked Norwegian fjord. II. Biomass and activity of net- and nanoplankton. Mar. Biol. 47: 313–323.

SMETACEK, V., K. VON BROCKEL, B. ZEITSCHEL, AND W. ZENK. 1978. Sedimentation of particulate matter during a phytoplankton bloom in relation to the hydrographical regime. Mar. Biol. 47: 211–226.

STEELE, J. H. 1974. The structure of marine ecosystems. Harvard University Press, Cambridge, MA.

SUSHCHENYA, L. M. 1962. Quantitative data on the feeding and energy balance of *Artemia saline* (L.). Dokl. Biol. Sci. Akad. Nauk USSR 143: 329–330.

TAGUCHI, S., AND M. FUKUCHI. 1975. Filtration rate of zooplankton community during spring bloom in Akkeshi Bay. J. Exp. Mar. Biol. Ecol. 19: 145–164.

TAGUCHI, S., AND T. PLATT. 1978a. Phytoplankton biomass in Bedford Basin: volume, surface area, carbon content and size distribution. Fish. Mar. Serv. Data Rep. No. 55: 404 p.

1978b. Size distribution and chemical composition of particulate matter in Bedford Basin, 1973 and 1974. Fish. Mar. Serv. Data Rep. No. 56: 370 p.

THOM, R., A. HAMPE, AND G. SAUERBEY. 1969. Die elektronische Volumenbestimmung von Blutkorperchen und ihre Fehlerquellen. Z. Gesamte Exp. Med. 191: 331–349. (Trans. ANL-TRAN-850, Scientific Translation Service, Ann Arbor, MI.)

WILSON, D. S. 1973. Food size selection among copepods. Ecology 54: 909–914.

Distribution of Digestive Enzymes in Zooplankton during the Spring Bloom in a Nova Scotia Inlet

P. Mayzaud

Biochimie Marine, Station Zoologique, 06230 Villefranche-sur-Mer, France

and R. J. Conover

Marine Ecology Laboratory, Bedford Institute of Oceanography, Dartmouth, N.S. B2Y 4A2

Mayzaud, P., and R. J. Conover. 1984. Distribution of digestive enzymes in zooplankton during the spring bloom in a Nova Scotia inlet. Can. J. Fish. Aquat. Sci. 41: 245–252.

Nonparametric correlation and principal component analysis were used to examine relations between digestive enzyme activity in zooplankton and qualitative and quantitative measures of particulate organic matter and between enzymes and composition of the zooplankton community. Barnacle nauplii in near-surface (5 m) water during the first part of the bloom caused heterogeneity, which confounded relationships between enzyme activity and potential substrate concentration. Lack of coherence among enzymes in the 5 m zooplankton was also observed. The less variable deepwater community showed intercorrelation among the enzymes measured. At 30 m, enzyme concentrations in *Pseudocalanus* were correlated with concentration of particles less than 20 μm, which were dominant in the first part of the bloom. Two time-related events significantly affected zooplankton enzyme levels: one was clearly related to the period of dominance of barnacle larvae and the other with an increase in the C:N ratio from around 5 to greater than 7 in midbloom coinciding with a shift in phytoplankton from smaller forms of apparently higher protein content to large colonial diatoms. The results generally support the hypothesis that the amount and chemical composition of food supply can affect zooplankton digestive enzymes, but they also demonstrate the problems of interpretation if community structure is not well defined and spatial and temporal distribution of organisms not carefully circumscribed.

L'analyse des corrélations non paramétriques et celle des composantes principales ont été utilisées pour examiner les relations existantes entre d'une part l'activité des enzymes digestives dans le zooplancton et les mesures qualitatives et quantitatives de la matière organique particulaire, et d'autre part entre les enzymes et la composition de la communauté zooplanctonique. Des nauplii de balanes dans l'eau près de la surface (5 m) pendant la première partie de la floraison ont causé une hétérogénéité qui a masqué les relations entre l'activité enzymatique et la concentration de substrats potentiels. On a observé également un manque de cohérence entre les enzymes dans le zooplancton récolté à 5 m. La communauté moins variable vivant en eau profonde a montré une intercorrélation entre les enzymes mesurées. À 30 m, les concentrations d'enzymes chez *Pseudocalanus* ont été corrélées avec la concentration de particules d'un diamètre inférieur à 20 μm, qui dominaient dans la première partie de la floraison. Deux événements temporels ont fait varier notablement les niveaux d'enzymes du zooplancton : l'un était nettement lié à la période de dominance de larves de balanes, l'autre à une augmentation du rapport C : N d'une valeur de 5 à plus de 7 au milieu de la floraison, coïncidant avec un changement dans le phytoplancton, qui passait de formes plus petites, apparemment plus riches en protéines, à de grandes diatomées coloniales. Les résultats obtenus appuient généralement l'hypothèse selon laquelle la quantité et la composition chimique des apports nutritionnels peuvent affecter les enzymes digestives du zooplancton, mais ils révèlent aussi les problèmes d'interprétation si la structure des communautés n'est pas bien définie et si la distribution spatiale et temporelle des organismes n'est pas correctement circonscrite.

Received December 29, 1982
Accepted October 12, 1983

Reçu le 29 décembre 1982
Accepté le 12 octobre 1983

An organism is normally exposed to environmental variation. Extremes in some factors may kill it outright, but for each variable there is a range within which it can survive. Response of the organism to change is also influenced by the duration of exposure. Some environmental events that initially cause accelerated activity, or even shock, with continued exposure, can be compensated for through acclimation over a period of a few days or weeks. Prolonged stress can result in adaptation through genetic selection over some generations.

There is an abundant literature pertaining to the ability of organisms to acclimate to temperature. Such an environmental event will probably precipitate an endocrine or neural response leading to increased protein and nucleic acid synthesis followed by production of new ribosomes and new isozymes (Somero and Hochachka 1971). While the patterns are not always consistent, there is evidence for induction or seasonal variation in activity of enzymes involved with intermediary metabolism in response to temperature (Livingstone 1981; Shaklee et al. 1977; Walsh and Somero 1981).

Much less is known about how animals respond to variability in the food supply. Energy storage as lipid, resting eggs, and arrested development are relatively long-term adaptations to reduced nourishment shown by planktonic copepods as well as

by many other aquatic invertebrates. For zooplankton the time of exposure is an important consideration in predicting the response of the animals to a variable food supply (Mayzaud and Poulet 1978). In Bedford Basin, N.S., they found that the activities of six digestive enzymes in a mixed zooplankton community were positively correlated with concentration of several substrates during the warmer months of the year. It took several days to induce laminarinase in *Euphausia pacifica* and *Calanus pacificus* when the right substrate was available (Cox 1981; Cox and Willason 1981). If time to induce the necessary digestive enzymes is a factor in adaptation to increasing particulate food, as postulated by Mayzaud and Poulet (1978), enzyme activity and food supply should be correlated during a period of accelerating primary production such as occurs during a phytoplankton bloom.

Here, we examine the digestive enzymes of the zooplankton community during the spring bloom in Bedford Basin during February–May 1977. In a companion paper we describe the feeding behavior of this zooplankton community during the same period (Conover and Mayzaud 1984).

Materials and Methods

Experimental animals and water were usually gathered from a regularly sampled station near the center of Bedford Basin, but on two occasions additional stations were sampled to give information on spatial variability. For a description of this environment, see Poulet (1973). Methods of capturing and handling the experimental material are given in Conover and Mayzaud (1984).

Replicate samples of zooplankton from the same population used to measure grazing were blended with a Sorvall omnimixer in redistilled acetone at −40°C, in proportions of 5 g of plankton to 100 mL of cold acetone, after removal of excess seawater by filtration on bolting cloth and blotting with filter paper. After rinsing the grinder with more cold acetone, the mixture was brought up to 150 mL in a 250-mL Erlenmeyer flask and allowed to stand in crushed ice for 90 min to ensure dehydration. Contents of the flask were then filtered and the residue was treated with the same volume of acetone at room temperature for 10 min, refiltered, and dried at −20°C in a desiccator under vacuum. The resultant "acetone powder" can be kept for months at −20°C without loss of enzyme activity. Analyses of amylase, maltase, cellobiase, laminarinase, and acidic and alkaline proteases were carried out at the Station Zoologique, Villefranche-sur-Mer, France, using procedures described in detail in Mayzaud (1980) and in Mayzaud and Mayzaud (1981).

Multivariate Statistical Analysis

Preliminary analyses were performed using nonparametric Spearman correlations, as described by Tate and Clelland (1957). Because bivariate correlation analysis describes the dominant seasonal associations rather than the day-to-day variability and does not take into account all the interrelations of the variables, a multivariate approach was found to be necessary to compare all data sets in three-dimensional space. Following the approach described by Legendre and Legendre (1979) a principal component analysis was performed on the correlation matrix of enzyme activity data. The elements of the resulting factor loading matrix are correlations between the original variables and the eigenvectors. Factor scores that represent weighted linear combinations of the enzyme activities are calculated to have zero mean and unit variance. The factorial axes may be interpreted using the elements of the factor loading matrix and the factor scores of the observations.

Once the factorial axes, based on the "active variables" (enzyme activities), have been extracted, "supplementary variables", not used in the determination of the axes, may be added to the analysis. The profile of these may be located on the projections using characteristic vectors derived from the active variables only. Formulations for computing supplementary variable projections may be found in Lebart et al. (1977).

Usually, a limited number of factors can be retained to explain a large proportion of the total variance. Projections of the variables or observations on the retained factorial planes may lead to the definition of groups of correlated variables or observations, which we will call "multivariate groups". To be considered valid such groups must be tight in all projections of the retained axes, and not in only one plane. Decisions regarding the formation of multivariate groups, although based on computed correlations between variables and the multivariate axes, are still rather subjective because of the difficulties of establishing the number of degrees of freedom to test correlation coefficients.

Normality of the data is not required for principal component analysis. Ibanez (1971) and Chanut et al. (1977) noted that the ordination of the variables on the first principal component is not necessarily modified by transformations of the original data. Nevertheless, a distortion occurs if some variables have a very different dispersion from others. They showed that stabilization or homogeneity of the variables accomplished by some appropriate transformation is sufficient to obtain consistent results. In our case, the sample variances of the enzyme profiles did not conform with the hypothesis of homogeneity. Logarithmic transformation stabilized the variances but did not modify the results of the analysis. Thus, we decided to avoid data transformation to describe and plot a set of real data points in a multidimensional space.

All computations were made on a Hewlett-Packard 9835 computer, using the programme from Lebart et al. (1977) as modified by Ph. Laval (Station Zoologique, Villefranche-sur-Mer).

Results

Collectively the distribution of protein-specific digestive enzymes in the zooplankton showed no obvious pattern (Fig. 1). At times the near-surface and deeper populations responded in an opposite manner on a given date. For example, the enzymes in the deep group all increased on March 10 or 11, while none of the enzymes from upper layer animals showed this response. Almost all measures of the standing crop of organic matter show a peak between March 10 and March 15 including total particle volume, primary production, and the C:N ratio (Fig. 2). Perhaps differences in zooplankton community structure, especially over the first portions of the bloom when barnacle nauplii were overwhelmingly dominant near the surface (Fig. 3), contributed to vertical differences in digestive enzymes. The deeper animals clearly showed much less variability in species composition over the experimental period than did upper water populations.

To clarify the complexity in the data, we examined first the relationships among specific enzyme activities in both surface and deep populations and then between the activities and a variety of independent variables describing aspects of the bloom and its associated zooplankton community using nonparametric Spearman rank correlation. The surface enzyme activities

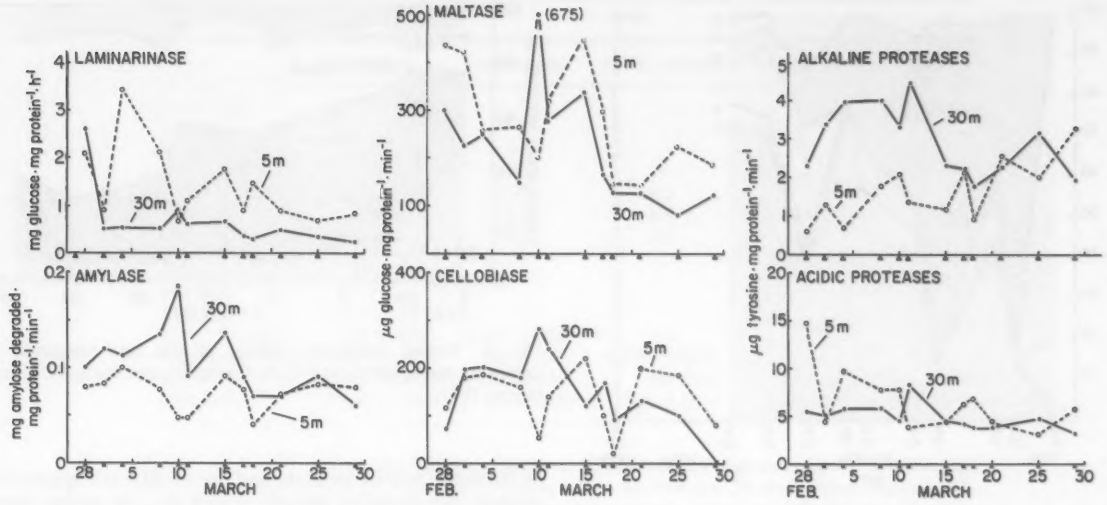


FIG. 1. Protein specific activity of six enzymes associated with the total euphotic zone plankton (5 m) and deepwater plankton (30 m) during the spring bloom of 1977 in Bedford Basin.

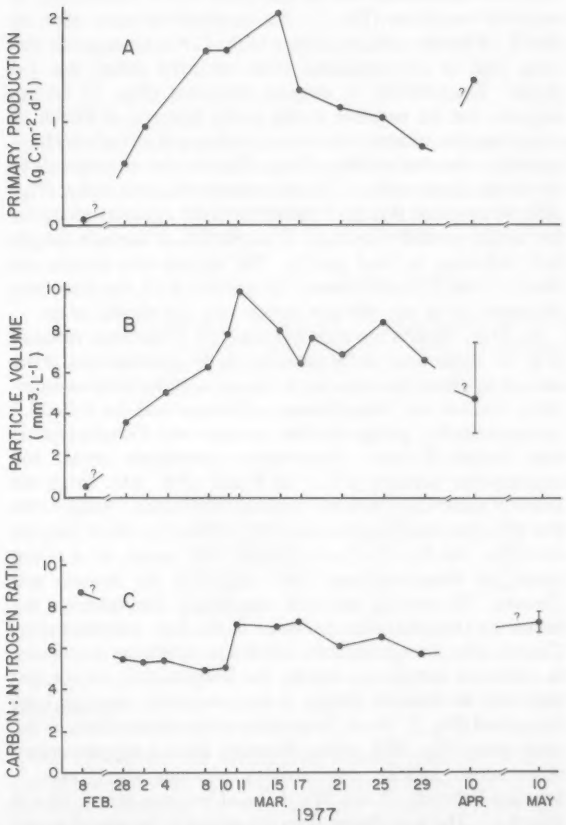


FIG. 2. Distribution of (A) daily primary production integrated for the water column (B) total particle volume at 5 m depth during the spring bloom, and (C) C:N ratio in particulate matter during the spring bloom, 1977, at 5 m.

showed almost no intercorrelations (Table 1), suggesting that some source of heterogeneity masked any interactions. In contrast, the 30-m enzyme activities were mostly well correlated, possibly indicating that digestive metabolism was the dominant source of variability. The correlation was improved by removing data from the first sampling date (Feb. 28, Table 1), some of which displayed activities higher than expected. In the second set of correlations (Table 2) the enzyme activities were compared with particulate organic carbon, particulate organic nitrogen, total volume of particles, and particulate matter in different size-classes as described by summing different Coulter counter channels. There were no significant relationships between enzyme concentrations and any measure of particulate biomass for the surface animals, but the 30-m populations displayed correlation between the carbohydrases (amylase, laminarinase, maltase, cellobiase) and the 8.0- to 20.2-µm particles, which accounted for the largest biomass peak during the first half of the bloom and remained important throughout March (Fig. 4). Composition of the deepwater zooplankton community did not influence enzyme distribution, whereas the abundance of certain near-surface species appeared to contribute to variability in laminarinase and both proteases (Table 3).

To further clarify the enzyme data in relation to the characteristics of the seston and zooplankton composition, correlation matrices were prepared and then subjected to principal component analysis. The six enzymes were taken to be active variables and the seston and zooplankton characteristics were treated as supplementary variates. At 5 m, the first two axes accounted for 72% of the total variance, with the third axis (not shown) explaining 14% of the remainder. Projections of all the variables on the factorial plane derived from the first two components (Fig. 5A) tend to confirm the results of the correlation analysis. Two multifactorial groups can be differentiated, one corresponding to laminarinase, acidic protease, and barnacle nauplii and the other to alkaline protease, all the other constituents of the zooplankton community, and part of the seston characteristics. From the levels of correlation between

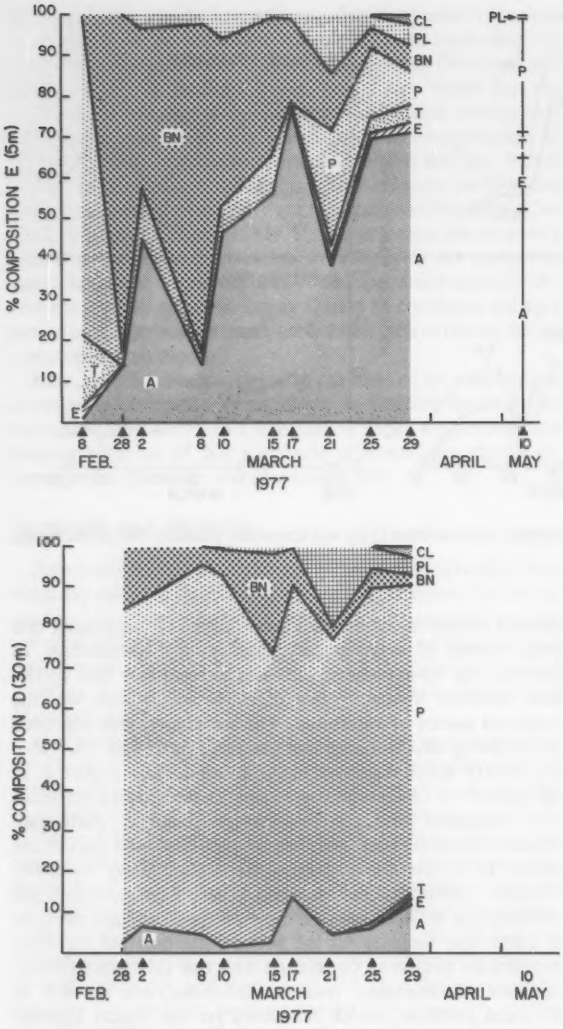


FIG. 3. Percentage composition of the zooplankton community in the euphotic zone (E, 5 m) and at 30 m (D) during the spring bloom, 1977. T, *Temora longicornis*; E, *Eurytemora herdmani*; A, *Acartia hudsonica*; P, *Pseudocalanus* sp.; BN, barnacle nauplii; PL, polychaete larvae; CL, cladocerans.

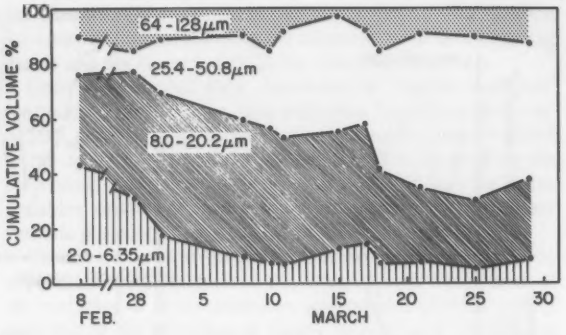


FIG. 4. Percent cumulative volume of four size categories of particulate matter measured with the Coulter counter during the spring bloom, 1977.

variables and the eigenvectors (Table 4), the first axis opposes (as shown by the different signs): (1) alkaline protease to the rest of the enzymes, (2) medium-size (25.4–50.8 μm) to small-size (2.0–6.35 μm) particles, and (3) the proportions of copepods and polychaete larvae to barnacle nauplii. This first component should be considered as a factor of temporal heterogeneity, which describes the degree of difference in enzyme activity profiles of variation and, to a minor extent, those of the particulate matter and zooplankton composition. Thus, the influence of the temporal heterogeneity on these latter two parameters would appear to have confounded any relationships between enzyme and food supply. The second axis, independent of the first, discriminates between acid protease, on the one hand, and cellobiase, on the other, but not between any supplementary variables. Projections of the dates of observation on the same factorial plane showed that the first axis appears to separate two sampling periods temporally, the period from February 28 to March 8 and that from March 10 to 28, with the exception of March 15 (Fig. 6B). Although still numerous, the barnacle nauplii had begun to decrease by March 10, suggesting that their distribution was an important factor contributing to temporal variability (Fig. 3). No zooplankton were taken on March 11 but the striking change in the C:N ratio suggests that some kind of environmental event occurred during this 1-d period. Examination of enzyme activities (Fig. 1) further suggests that the negative scores on the first axis of March 10 and 11 are also related to the strong decrease in all carbohydrase activities observed on these dates. Since it also corresponds to the abrupt change in the C:N ratio of the particulate matter (Fig. 2C), we conclude that the distribution of the variables along the first axis is related to changes in proportion of barnacle nauplii and variations in food quality. The second axis singles out March 15 and 25 from February 28 and March 18, but there does not appear to be any obvious reason why this should be so.

At 30 m, the first two axes explain 92% of the total variance (Fig. 6). Projections of the variables on the multifactorial plane defined by these two axes show several multifactorial associations: maltase and laminarinase; cellobiase and the 8.0–20.2 μm particle size group; alkaline protease and *Pseudocalanus*; and *Acartia*, *Temora*, *Eurytemora*, polychaete larvae, and medium-size particles (25.4–50.8 μm) (Fig. 6A). From the levels of correlation between variables and factors (Table 5) the first principal component is positively defined by all six enzyme activities, the 8.0–20.2 μm particle size group, to a minor extent by *Pseudocalanus*, and negatively by *Acartia* and *Temora*. The second principal component discriminates between the two proteases and three of the four carbohydrases. Conceivably, it might indicate a shift from herbivore dominance to carnivore dominance among the zooplankton, except that there was no dramatic change in the community structure over this period (Fig. 3, 30 m). Projections of the observations on the same plane (Fig. 6B), taking February 28 as a supplementary observation, indicate two striking changes along axis 2: between February 28 and March 2 and between March 10 and March 11. The first change does not appear to be related to any variable that we measured, but the second coincides with the sudden increase in the C:N ratio in the particulate matter (Fig. 2C), suggesting an abrupt change in food quality presumably toward proportionately greater production of carbohydrate.

TABLE 1. Values of t for the Spearman rank correlations of the digestive enzyme activities from the total near-surface and 30-m samples (t values in parentheses have the February 28 observations omitted). NS, nonsignificant at the 0.05 level.

	Amylase	Laminarinase	Acidic protease	Alkaline protease	Maltase
5 m, df = 10					
Amylase	—				
Laminarinase	NS	—			
Acidic protease	NS	2.469	—		
Alkaline protease	NS	−2.976	NS	—	
Maltase	NS	NS	NS	NS	—
Cellobiase	2.699	NS	NS	NS	NS
30 m, df = 10(9)					
Amylase	—				
Laminarinase	4.078 (5.885)	—			
Acidic protease	NS (2.258)	2.453 (2.285)	—		
Alkaline protease	2.820 (2.545)	NS (2.292)	6.098 (8.686)	—	
Maltase	3.506 (3.468)	5.205 (4.612)	NS (NS)	—	
Cellobiase	2.380 (2.728)	NS (3.548)	NS (3.031)	3.739 (3.901)	

TABLE 2. Values of t for the Spearman rank correlations between digestive enzyme activities and particulate matter variables (t values in parentheses have the February 28 observations omitted). NS, nonsignificant at the 0.05 level; Partial particle volume, particle volume in different size classes as determined with the Coulter counter; VOL, total particle volume measured with the Coulter counter; POC, particulate organic carbon; PON, particulate organic nitrogen. There was no significant correlation at 5 m, df = 10.

	Partial particle volume: equivalent spherical diameter (μm)						
	2.0–6.35	8.0–20.2	25.4–50.8	64.0–128	VOL	POC	PON
30 m, df = 10(9)							
Amylase	NS	2.560 (2.860)	NS	NS	NS	NS	NS
Laminarinase	2.295 (NS)	NS (3.652)	NS	NS	NS	NS	NS
Acidic protease	NS	NS (NS)	NS	NS	NS	NS	NS
Alkaline protease	NS	NS (NS)	NS	NS	NS	NS	NS
Maltase	3.198 (NS)	2.690 (4.529)	NS	NS	NS	NS	NS
Cellobiase	NS	3.284 (2.728)	NS	NS	NS	NS	NS

TABLE 3. Values of t for the Spearman rank correlations between digestive enzyme activities and zooplankton composition as % of the total population. NS, nonsignificant at the 0.05 level. There was no significant correlation at 30 m, df = 10.

	Acartia	*Pseudocalanus*	Barnacle nauplii	*Eurytemora*	*Temora*	Polychaete larvae
5 m, df = 10						
Amylase	NS	NS	NS	NS	NS	NS
Laminarinase	−3.034	NS	4.176	−2.888	NS	NS
Acidic protease	NS	NS	2.561	NS	NS	NS
Alkaline protease	NS	NS	−2.811	3.261	2.839	NS
Maltase	NS	NS	NS	NS	NS	NS
Cellobiase	NS	NS	NS	NS	NS	NS

Discussion

Our hypothesis that zooplankton feeding rates are in some way associated with induction of digestive enzymes is based on the results obtained by Mayzaud and Conover (1976) and Mayzaud and Poulet (1978). Although their data were gathered in the same environment, they were obtained during the summer period characterized by stability in the water column and small variance in the composition and abundance of the food supply and, to a lesser extent, in the zooplankton composition. In designing this experiment we expected important changes in quantity and quality of the phytoplankton produced during the spring bloom (Conover and Mayzaud 1984), but we did not anticipate the magnitude of changes in zooplankton community structure that took place. The brief dominance of barnacle nauplii in the near-surface layers, presumably growing rapidly

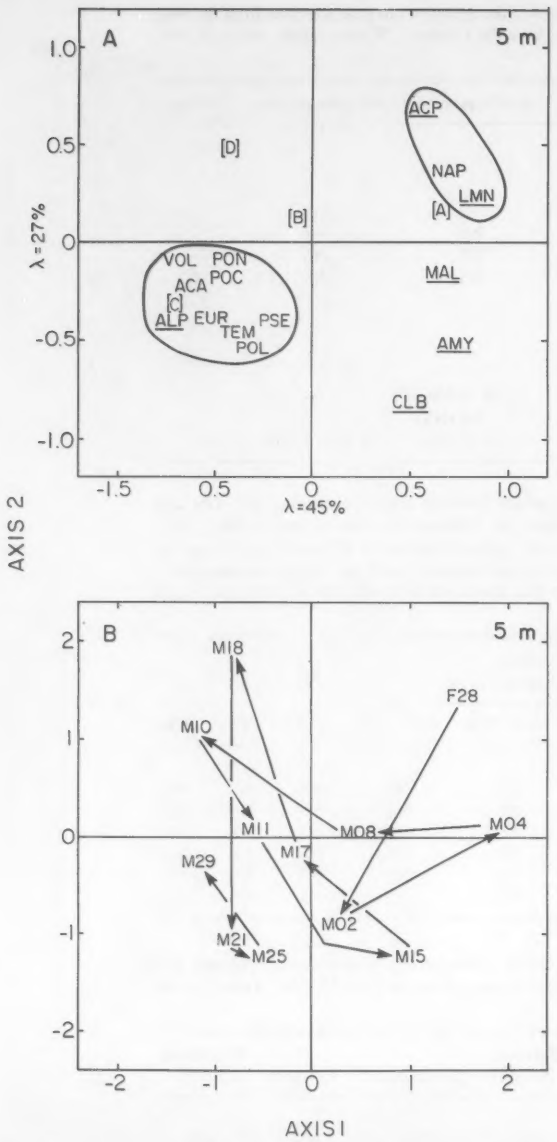


FIG. 5.(A) Associations for the 5 m population (based on principal component analysis) between the variables, including six enzymes, seston characteristics, and composition of the zooplankton population. Projections are in the factorial plane of the primary axes (C_1 and C_2). The underlined variables are active. The encircled groupings are multifactorial groups valid in all other planes of projection. AMY, amylase; LMN, laminarinase; MAL, maltase; CLB, cellobiase; ACP, acidic protease; ALP, alkaline protease; [A], volume of particles in size range 2–6.4 μm equivalent spherical diameter (ESD); [B], volume of particles 8–20.2 μm ESD; [C], volume of particles 25.4–50.8 μm ESD; [D], volume of particles 64–128 μm ESD; VOL, total volume; POC, particulate organic carbon; PON, particulate organic nitrogen; NAP, barnacle nauplii; ACA, *Acartia hudsonica*; PSE, *Pseudocalanus* sp.; EUR, *Eurytemora herdmani*; TEM, *Temora longicornis*; POL, polychaete larvae; λ, % of the total variance explained by the axis. (B) Associations, based on the same method of analysis, between the dates of observations. F, February; M, March; number, date.

TABLE 4. Correlation coefficients between active and supplementary variables and the first three multivariate axes (factor loadings) for the 5-m data matrix.

Variable	Factor 1	Factor 2	Factor 3
Amylase	0.718	−0.525	−0.313
Laminarinase	0.836	0.238	−0.400
Acidic protease	0.570	0.682	−0.161
Alkaline protease	−0.720	−0.398	−0.321
Maltase	0.632	−0.165	0.689
Cellobiase	0.485	−0.810	−0.033
(2–6.4 μm)	0.662	0.165	0.510
(8–20.2 μm)	−0.071	0.121	0.424
(25.4–50.8 μm)	−0.702	−0.344	−0.034
(64–128 μm)	−0.419	0.484	−0.408
VOL	−0.591	−0.143	0.179
POC	−0.473	−0.183	0.292
PON	−0.555	−0.125	0.069
Acartia	−0.612	−0.195	0.089
Pseudocalanus	−0.197	−0.389	−0.274
Barnacle nauplii	0.688	0.364	0.113
Eurytemora	−0.555	−0.387	−0.392
Temora	−0.393	−0.428	−0.467
Polychaete larvae	−0.341	−0.526	−0.319

in preparation for metamorphophosis to a shore-fast adult, confounded the interpretation of the behavior of the remaining semipermanent component of the population.

In the preceding paper (Conover and Mayzaud 1984) it was shown that ingestion rates of the surface zone zooplankton were positively correlated with the quantity of potential food in their immediate environment. If our hypothesis is correct, these animals ought to show a good correlation between food supply and enzyme activity, but they do not (Table 2). On the other hand, deeper living zooplankton, predominately *Pseudocalanus* sp., maintained a nearly constant rate of ingestion, despite changes in concentration of food offered to them. However, it was near-surface water, and not water from 30 m, that was used in the feeding experiments, so that the *Pseudocalanus*-dominated community might only encounter such high food concentration during diel migrations and therefore might be less well acclimated to these food conditions than surface forms. A nonparametric correlation analysis failed to show any relationship for *Pseudocalanus* with any enzyme at either depth, but the barnacles, primarily found in the upper layers, showed both positive and negative correlations there (Table 3).

Examining the variation among digestive enzymes, the 30-m animals show a high degree of metabolic coherence (Table 1), which is consistent with their relatively stable community structure (Fig. 3). Several enzymes from animals found below the euphotic zone were correlated with concentrations of particles in the < 20 μm category (Table 2), which was the dominant particle peak in the early part of the bloom (Fig. 4). According to Poulet (1974), *Pseudocalanus* in Bedford Basin gets most of its rations over the course of the year from smaller sized particles and from concentration peaks in the particle spectrum.

There was no internal correlation among enzymes in near-surface zooplankton, suggesting that causes other than dietary induction of digestive enzymes controlled their activity. Both correlation and principal component analysis suggest that a large and variable population of young barnacles with large

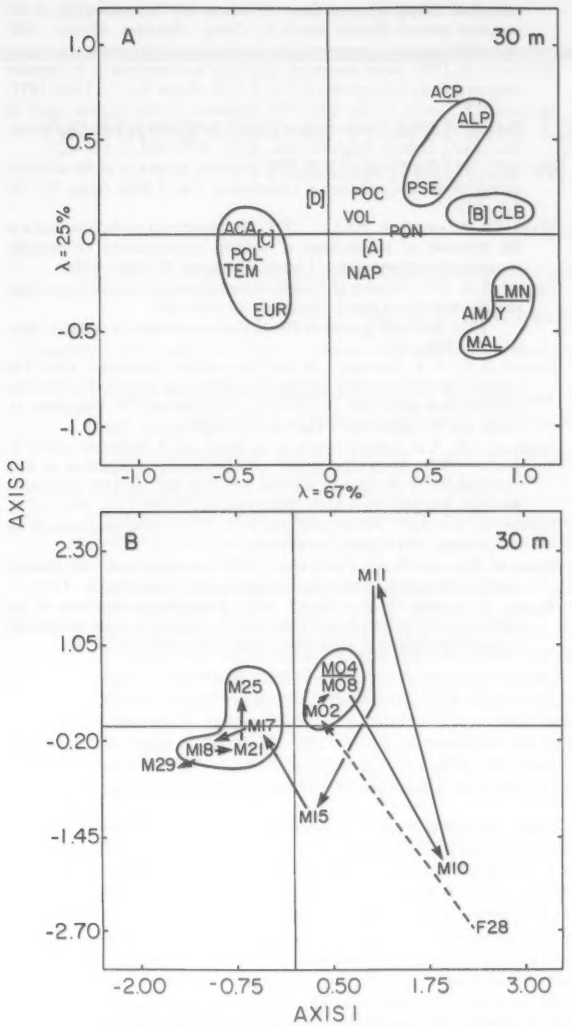


FIG. 6.(A) Associations for the 30 m populations (based on principal component analysis) between the variables, including six enzyme activities, seston characteristics, and composition of the zooplankton population. Projections are in the factorial plane of the primary axes (C_1 and C_2). Symbols as for Fig. 6A. (B) Associations, based on the same analysis, between the dates of observations. The encircled groupings are multifactorial groups valid in all other planes of projection. Symbols as for Fig. 6B.

enzyme concentrations is the principal cause of enzyme variability in all but alkaline protease.

Principal component analysis suggested several other interactions between organisms and food supply. For instance, opposition on the first axis between small- and medium-size particles at 5 m (Fig. 5A) implies partitioning of the food supply between barnacles and the remaining zooplankton species. The discrimination, by the second axis, of protease from three out of four carbohydrases in the deepwater community (Fig. 6A) suggests some shift in feeding by the *Pseudocalanus*-dominated community from a largely protein to a carbohydrate diet.

Time analysis suggests that important events occurred in both shallow and deep layers over the course of the experiment. In the 5-m community the primary axis implies breaks in continuity of enzymes after March 8 and again around March 15 (Fig. 5B) that coincide reasonably well first with an abrupt change in the C:N ratio of the food supply and second with a significant reduction in barnacle naupliar dominance (Fig. 3). For *Pseudocalanus*, a major event took place between March 10 and 11 that coincided with a shift in the C:N ratio (Fig. 2C) and with the probable shift in enzyme dominance mentioned above. All these events apparently reflect a shift in particle size dominance and phytoplankton species composition in the surface water wherein smaller, more protein-rich species of phytoplankton are partially replaced by larger, carbohydrate-rich, colonial diatoms (Conover and Mayzaud 1984).

Although our spring bloom data were much more complex than those described by Mayzaud and Conover (1976), there is still a strong suggestion that food supply and digestive enzyme complement are related in zooplankton, at least in the long run. That this relationship can have different times scales at different seasons and temperatures for a single species is shown by recent work on the large arctic copepod *Calanus hyperborus* (Head and Conover 1983). Nevertheless, when the total population is considered, the enzyme levels are controlled not only by the quality and quantity of food supply but also by the presence in that population of different growth stages with different intensities of enzyme expression (Samain et al. 1980; Hirche 1981; P. Mayzaud, unpubl. data) corresponding to different physiological needs. Furthermore, because each organism presumably integrates events affecting only itself under the constraints of a genetically imposed scope for activity, pooling too many trophic types, e.g. by analyzing the entire contents of a vertical plankton haul, can only result (through confounding) in a serious information loss.

TABLE 5. Correlation coefficients between active and supplementary variables and the first three multivariate axes (factor loadings) for the 30-m data matrix.

Variable	Factor 1	Factor 2	Factor 3
Amylase	0.862	−0.383	0.304
Laminarinase	0.931	−0.285	−0.045
Acidic protease	0.617	0.752	−0.109
Alkaline protease	0.745	0.613	0.207
Maltase	0.798	−0.539	−0.151
Cellobiase	0.924	0.113	−0.203
(2–6.4 μm)	0.233	−0.075	−0.286
(8–20.2 μm)	0.777	0.109	−0.271
(25.4–50.8 μm)	−0.374	−0.007	−0.196
(64–128 μm)	−0.063	0.192	−0.304
VOL	0.128	0.093	−0.366
POC	0.113	0.148	−0.549
PON	0.371	−0.003	−0.338
Acartia	−0.492	0.010	−0.064
Pseudocalanus	0.488	0.241	0.142
Barnacle nauplii	0.176	−0.204	0.126
Eurytemora	−0.316	−0.390	0.208
Temora	−0.487	−0.180	0.015
Polychaete larvae	−0.433	−0.108	−0.265

Acknowledgments

We are grateful to M. Paranjape for his assistance in the field

and laboratory and to M. Huntley for preparing the enzyme samples. We also thank J. Fournier and J. Chiaverini for their help with analyses and J. P. Chanut (University of Quebec at Rimouski) for valuable statistical advice. This work was partially supported by NATO Grant No. 1401.

References

CHANUT, J. P., S. A. POULET, D. COSSA, AND J. C. MARTY. 1977. Factor analysis of the suspended matter distribution in the St. Lawrence estuarine system, p. 1–23. Proceedings of the 1st World Conference on Mathematics at the Service of Man, Barcelona, Spain.

CONOVER, R. J., AND P. MAYZAUD. 1984. Utilization of phytoplankton by zooplankton during the spring bloom in a Nova Scotia inlet. Can. J. Fish. Aquat. Sci. 41: 0000–0000.

COX, J. L. 1981. Laminarinase induction in marine zooplankton and its variability in zooplankton samples. J. Plankton Res. 3: 345–356.

COX, J. L., AND S. W. WILLASON. 1981. Laminarinase induction in *Calanus pacificus*. Mar. Biol. Lett. 2: 307–311.

HEAD, E. J. H., AND R. J. CONOVER. 1983. Induction of digestive enzymes in *Calanus hyperboreus*. Mar. Biol. Lett. 4: 219–231.

HIRCHE, H. J. 1981. Digestive enzymes of copepodids and adults of *Calanus finmarchicus* and *C. helgolandicus* in relation to particulate matter. Kiel. Meeresforsch. 5: 174–185.

IBANEZ, F. 1971. Effet des transformations des données dans l'analyse factorielle en écologie planctonique. Cah. Oceanogr. 23: 545–561.

LEBART, L., A. MORINEAU, AND N. TABARD. 1977. Technique de la description statistique. Dunod, Paris. 351 p.

LEGENDRE, L., AND P. LEGENDRE. 1979. Ecologie numérique. 2. La structure des données écologiques. Masson, Montreal. 247 p.

LIVINGSTONE, D. R. 1981. Induction of enzymes as a mechanism for the seasonal control of metabolism in marine invertebrates: glucose-6-phosphate dehydrogenases from the mantle and hepatopancreas of the common mussel *Mytilus edulis* L. Comp. Biochem. Physiol. 69B: 147–156.

MAYZAUD, P. 1980. Some sources of variability in determination of digestive enzyme activity in zooplankton. Can. J. Fish. Aquat. Sci. 37: 1426–1432.

MAYZAUD, P., AND R. J. CONOVER. 1976. Influence of potential food supply on the activity of digestive enzymes of neritic zooplankton. 10th Eur. Symp. Mar. Biol., Ostend, Belgium, Sept. 7–23, 1975. Vol. 2: 415–427.

MAYZAUD, P., AND O. MAYZAUD. 1981. Kinetic properties of the digestive carbohydrases and proteases of zooplankton. Can. J. Fish. Aquat. Sci. 38: 535–543.

MAYZAUD, P., AND S. A. POULET. 1978. The importance of the time factor in the response of zooplankton to varying concentrations of naturally occurring particulate matter. Limnol. Oceanogr. 23: 1144–1154.

POULET, S. A. 1973. Grazing of *Pseudocalanus minutus* on naturally occurring particulate matter. Limnol. Oceanogr. 18: 564–573.

1974. Seasonal grazing of *Pseudocalanus minutus* on particles. Mar. Biol. 25: 109–123.

SAMAIN, J. F., J. Y. DANIEL, J. R. LE COZ, AND M. JEZEQUEL. 1980. The digestive enzymes amylase and trypsin during the development of *Artemia*: effect of food conditions, p. 225–235. *In* G. Persoone, P. Sorgeloos, O. Roels, and E. Jaspers [ed.] The brine shrimp *Artemia*. Vol. 2.

SHAKLEE, J. B., J. A. CHRISTIANSEN, B. D. SIDELL, C. L. PROSSER, AND G. S. WHITT. 1977. Molecular aspects of temperature acclimation in fish: contributions of changes in enzyme activities and isozyme patterns to metabolic reorganization in the green sunfish. J. Exp. Zool. 201: 1–20.

SOMERO, G. N., AND P. W. HOCHACHKA. 1971. Biochemical adaptation to the environment. Am. Zool. 11: 157–167.

TATE, M. E., AND R. C. CLELLAND. 1957. Non-parametric and shortcut statistics. Interstate Printers and Publishers, Inc., Danville, IL. 171 p.

WALSH, P. J., AND G. N. SOMERO. 1981. Temperature adaptation in sea anemones: physiological and biochemical variability in geographically separate populations of *Metridium senile*. Mar. Biol. 62: 25–34.

An Integration of Forest and Lake Fertilization: Transport and Transformations of Fertilizer Elements

C. J. Perrin

B.C. Ministry of Environment, Fish and Wildlife Branch, 2204 Main Mall, University of British Columbia, Vancouver, B.C. V6T 1W5

and K. S. Shortreed and J. G. Stockner

Department of Fisheries and Oceans, Fisheries Research Branch, West Vancouver Laboratory, 4160 Marine Drive, West Vancouver, B.C. V7V 1N6

Perrin, C. J., K. S. Shortreed, and J. G. Stockner. 1984. An integration of forest and lake fertilization: transport and transformations of fertilizer elements. Can. J. Fish. Aquat. Sci. 41: 253–262.

Forest fertilization (435 kg urea·ha^{-1}) on the Mohun drainage, northern Vancouver Island, during late fall 1979 resulted in a combined increase in urea, ammonia, and nitrate concentrations to 8000 μg N·L^{-1} above control levels in streams not protected with 50-m-wide leave (i.e. unfertilized) strips and 350 μg N·L^{-1} in those having leave strips. By spring 1980, dissolved nitrogen loads to Mohun Lake increased by a minimum of 55% in the largest basin and 1924% in the smallest basin. This corresponded to fertilizer losses of 2.1% of the total applied from drainages that had leave strips and up to 5.2% from those where the treatment included direct application to stream channels. Nitrogen transport was dominated by reduced nitrogen species and lasted up to 144 d. Relatively small changes in nitrate transport were attributed to low temperatures, which reduced rates of nitrification. During the 3-yr prior to forest fertilization, nitrogen and phosphorus were added to the lake at an N:P ratio of 4.5 (wt/wt) and a load of 1.4–2.2 mg P·m^{-2}·wk^{-1}. Spring overturn phosphorus concentrations were 4–5 μg·L^{-1} throughout the study and, except during the spring following forest fertilization, N:P ratios (NO_3-N:TP) at spring overturn were 3–6 (wt/wt). Despite the low ratios, nitrogen-fixing phytoplankton were not dominant in Mohun Lake. After forest fertilization, average epilimnetic chlorophyll concentrations were 1.8 times higher than in 1979, the last year of lake fertilization. The increase is attributed to the much higher spring overturn N:P ratio that occurred after forest fertilization and to phosphorus recycling processes within the extensive littoral zone of the lake.

La fertilisation de la forêt (435 kg d'urée·ha^{-1}) dans le bassin de drainage du lac Mohun, au nord de l'île Vancouver à la fin de l'automne 1979, a entraîné une augmentation combinée des concentrations d'urée, d'ammoniaque et de nitrates jusqu'à 8000 μg N·L^{-1} au-dessus des niveaux de contrôle dans les cours d'eau non protégés par des bandes vierges (c.-à-d. non fertilisées) larges de 50 m, et jusqu'à 350 μg N·L^{-1} dans ceux qui ont des bandes vierges. Au printemps 1980, les apports d'azote dissous dans le lac Mohun ont augmenté d'au moins 55 % dans le bassin le plus grand et de 1924 % dans le bassin le plus petit. Cela correspondait à des pertes d'engrais de 2,1 % du total appliqué provenant des bassins de drainage qui ont des bandes vierges et jusqu'à 5,2 % provenant de ceux où le traitement incluait l'application directe jusqu'aux cours d'eau. Le transport d'azote s'est fait surtout sous forme de composés d'azote réduits et il a duré jusqu'à 144 jours. Les changements relativement petits dans le transport des nitrates ont été attribuées aux basses températures qui ont réduit les taux de nitrification. Au cours des 3 années précédant la fertilisation de la forêt, de l'azote et du phosphore ont été ajoutés au lac dans un rapport N:P de 4,5 (pds/pds) et un apport de 1,4 à 2,2 mg P·m^{-2}·sem^{-1}. Les concentrations de phosphore au cours du mouvement de descente des eaux au printemps ont varié de 4 à 5 μg·L^{-1} pendant toute l'étude et, sauf au cours du printemps suivant la fertilisation de la forêt, les rapports N:P (NO_3-N:PT) lors du mouvement de descente printanier ont varié de 3 à 6 (pds/pds). En dépit des rapports faibles, le phytoplancton fixateur d'azote n'était pas prédominant dans le lac Mohun. Après la fertilisation de la forêt, les concentrations moyennes de chlorophylle dans l'épilimnion ont été de 1,8 fois supérieures à celles de 1979, la dernière année de la fertilisation du lac. L'augmentation est attribuée à la hausse très nette du rapport N:P qui s'est produite après la fertilisation de la forêt, au moment du mouvement de descente printanier, et aux processus de recyclage du phosphore à l'intérieur de la vaste zone littorale du lac.

Received June 7, 1983
Accepted October 13, 1983

Reçu le 7 juin 1983
Accepté le 13 octobre 1983

Forest growth has been enhanced by the application of urea fertilizers in several North American studies (Miller et al. 1979; Safford and Filip 1974; Tarrant and Silen 1966). Similarly, experimental work on inorganic nitrogen and phosphorus enrichment of oligotrophic lakes in coastal British Columbia has shown that fertilization can enhance lake metabolism and increase sockeye salmon (*Oncorhynchus nerka*) growth and abundance (Le Brasseur et al. 1978; Stockner 1981). Several investigators (Fredriksen et al. 1974; Meehan et al. 1975; Moore 1974, 1975; Stay et al. 1978) have found that nitrogen loading to streams after forest fertilization is minimal and not detrimental to stream water quality or biota. The nitrogen species transported to streams and lakes following forest treatments are the same as those that are added in

combination with phosphorus in lake fertilization experiments. To date, the fate of this nitrogen lost from land has not been quantified for lakes of British Columbia.

In 1979, a project was initiated to examine the consequences of nitrogen loading on Mohun Lake following forest fertilization with urea. Objectives of the study were to follow the transport and the transformations of fertilizer nitrogen in streams of the Mohun Lake drainage basin from October 1979 to April 1980, to document limnological conditions in Mohun Lake from 1977 to 1979, the period of experimental lake fertilization, and to examine the impact of residual forest fertilizer nitrogen loading on Mohun Lake metabolism during the 1980 growing season.

Study Area

The study was conducted on the Mohun Lake drainage basin (4773 ha) located on Vancouver Island approximately 30 km northwest of Campbell River, B.C. (Fig. 1). The dominant vegetation, 30 to 40-yr-old Douglas fir (*Pseudotsuga menziesii*), was thinned from about 2000 to 550 trees·ha^{-1} in 1977. All slash was left on the forest floor. Understory vegetation consists predominantly of salal (*Gaultheria shallon*) with occasional bracken fern (*Pteridium aqualinum*), huckleberry (*Vaccinium parvifolium*), fireweed (*Epilobium angustifolium*), and Oregon grape (*Mahonia nervosa*). Understory cover is about 15% under the forest canopy and 70–90% in open areas such as rocky knolls and upland clearings. Riparian vegetation close to outflows into Mohun Lake includes alder (*Alnus rubra*) and willow (*Salix* spp.), which provide about 80% canopy closure. Annual precipitation in the area ranges from 1050 to 1520 mm, with most occurring from late September to mid-March (Fig. 2).

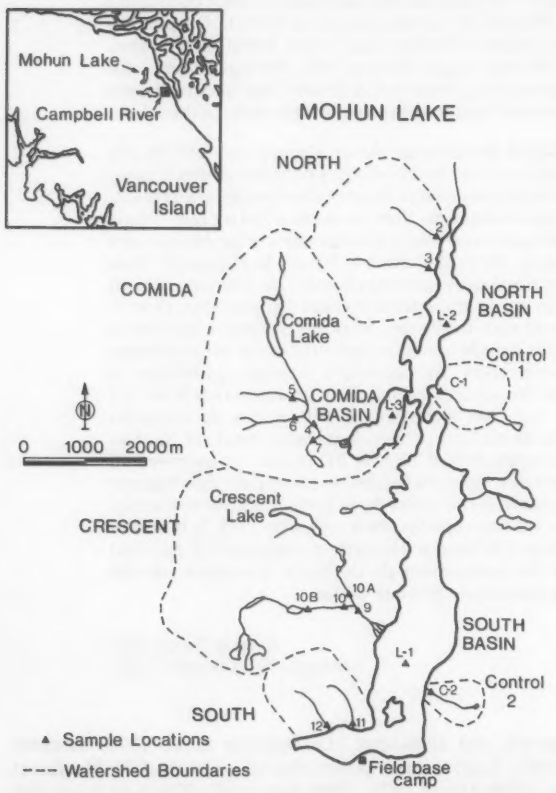


FIG. 1. Mohun Lake and associated drainages. Sample locations with the L prefix refer to lake basin locations, C prefix refers to control streams, and locations without a lettered prefix refer to treatment stream sample locations.

Bedrock is mainly composed of acid granitics, and outcrops occur in many locations at higher elevations on the west side of Mohun Lake. An impermeable marine clay overlies bedrock in northwest sections of the study area and has given rise to bog conditions. Soils are a shallow, well-drained, sandy loam with a well-developed surface organic layer varying in thickness from 3 to 14 cm. The loam has a high organic content and a high cation exchange capacity. The soils also contain macropores that act to quickly channel water through the soil matrix (Feller and Kimmins 1979).

Within the study area, four major drainages were fertilized: Mohun north (503 ha), Comida (996 ha), Crescent (960 ha), and Mohun south (105 ha) (Fig. 1). Two untreated controls (72 and 45 ha) were located on the east side of Mohun Lake, well removed from wind-carried fertilizer dust (Fig. 1). Within the study area, two stream types (I and II) were differentiated primarily on the basis of geomorphological characteristics and the presence of indicators that revealed a potential for nitrogen processing (Table 1). Several streams within the study area had both type characteristics and were classified as type I plus II streams. The number of streams in the study area was sufficient for replicate measurements of nitrogen transport to be completed for each combination of stream and treatment type. Mohun Lake has three discrete basins separated by narrow, shallow sills (Fig. 1). Basin volumes are 1.7×10^6, 8.2×10^6, and 7.9×10^7 m^3 for Comida and the north and south basins, respectively.

Materials and Methods

Fertilizer Applications

Forest fertilizer applications began on November 15, 1979, on the Mohun South drainage and proceeded northward to the final area, Mohun North, which was completed on December 3, 1979. The application rate was 435 kg urea·ha^{-1} (200 kg N·ha^{-1}). A Bell 205 A-1 helicopter equipped with computerized navigational equipment (Del Norte Transponder MS 12 Flying Flagman) to maintain accurate flight lines and treatment boundaries was used. Fertilizer was carried in a centrifugal spreader slung beneath the helicopter. The spreader had an

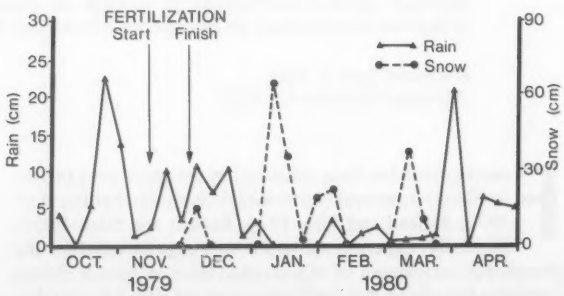


FIG. 2. Seasonal variation in weekly precipitation at Mohun Lake.

TABLE 1. Criterion used in stream type differentiation.

Differentiation factor	Significance of factor	Stream type I, steep whitewater	Stream type II, marsh
Gradient	Higher gradients can result in high stream power, which inhibits deep accumulation of fine particulate organic matter (FPOM)	> 1%	< 1%
Substrate type	Deep sediment accumulations may indicate potential for nitrogen immobilization and denitrification. Gravel and cobble substrates indicate rapid nutrient turnover or direct transport to downstream ecosystems	Gravel, cobble, boulders. Localized debris dams	Deep sediment (FPOM) in a mud consistency throughout
Associated vegetation	Marsh and bog macrophytes may indicate active nitrogen sinks (plant uptake, denitrification, immobilization) and slow nutrient turnover to downstream ecosystems. Periphyton accumulations on gravel and cobble may be active in rapid recycling of nitrogen to downstream ecosystems by cyclical particle size transformations.	Few aquatic macrophytes. Mostly limited to algal accumulations not visually obvious on the gravel, cobble, and boulder substrate	Abundant aquatic macrophytes including bog species

output capacity of 2041 $kg \cdot min^{-1}$ and covered a swath width of 61 m. Leave strips (zones that did not receive treatment) 50 m wide were maintained on the lake margin and along streams visible from the air in the Crescent drainage. To determine leave strip effectiveness, three fertilizer sampling transects were laid out across leave strip boundaries. The 50-m-long transects were 50 m apart, and half of each transect was within the leave strip. At 10-m intervals along each transect, samplers consisting of a plastic bag hung from a 0.48-m-diameter aluminum hoop were placed 0.75 m off the ground. After fertilization, pellets within each bag were counted and results were converted to weight per unit area.

Mohun Lake was fertilized from April 15, 1977, until October 1979 with ammonium nitrate (NH_4NO_3) and ammonium phosphate ($(NH_4)_3PO_4$) at an N:P ratio of 4.5 (by weight). The application rate in 1977 and 1978 was 2.2 mg $P \cdot m^{-2} \cdot wk^{-1}$ and in 1979 it was reduced to 1.4 mg $P \cdot m^{-2} \cdot wk^{-1}$. The fertilizer solution was applied to the surface waters of the Mohun Lake south basin once weekly commencing on April 15 for 26 wk each year.

Stream Sampling

Staff gauges were established on each of the study streams and gauge heights were regularly recorded. Spot flow measurements were also taken to calculate stream discharges.

Stream water samples were collected from March 1979 to May 1980 (430 d). To simplify statistical analyses, sampling at each location was separated into five steps. First, monthly pretreatment sampling began 8 mo prior to forest fertilization and continued to October 1979. Step 2 included the first 3 d following treatment. This consisted of 2-h intervals in the first day, 4-h intervals during day 2, and 6-h intervals in day 3. Step 3 included two samples per day over days 4–6 after treatment, once per day for the next 6 d, and every second day for an additional 6 d. Samples were collected twice a week in step 4 for the next 40 d (19–59 d after treatment). Weekly samples were collected thereafter in step 5 until study completion.

All samples were collected in acid-rinsed, 1-L polyethylene bottles, placed in coolers, and shipped to the Environmental Laboratory of the B.C. Ministry of Environment, Vancouver, B.C., for analysis within 24 h of collection.

All samples were analyzed for nitrate nitrogen (NO_3-N), ammonia nitrogen ($NH_3 + NH_4$), and urea nitrogen (H_2NCONH_2). Nitrate was determined by cadmium reduction plus diazotization (Strickland and Parsons 1972; APHA 1976). Ammonia was analyzed by the automated colorimetric method (Traversy 1971). Urea was also determined colorimetrically by reaction with diacetylmonoxine (Kluckner et al. 1980). In this study dissolved nitrogen (DN) was the sum of nitrate nitrogen, ammonia nitrogen, and urea nitrogen.

Stream type (I, II, and I + II), treatment (control, leave strip presence, and leave strip absence), and time (five steps as described above) were used in an ANOVA to detect significant differences ($P < 0.05$) in stream DN concentrations.

Measurement of Nitrogen Loss from the Drainage Areas

When peak levels of DN occurred in each lake basin, the weight of nitrogen in each depth strata was calculated by multiplying the DN concentration by the corresponding volume of each depth strata. Summation of strata loads gave total weight of nitrogen for each lake basin. The nitrogen load from fertilizer inputs was the difference between the DN load after treatment and the mean nitrogen load during the same month of pretreatment years. This method integrated inputs from groundwater as well as streams.

Calculated nitrogen loads are underestimates of actual loads because (1) the method used does not account for nitrogen sinks or lake outflow loss and (2) calculations are assumed to reflect accumulated loadings up to peak concentrations and do not include residual loading that may have occurred after peak concentrations were measured.

Lake Sampling

Mean weekly air and lake surface temperatures and weekly total precipitation data for the study area were provided by the Atmospheric Environment Service, Environment Canada, Campbell River Station. Weekly rain and snow accumulations were obtained with a Weather Measure Corp. standard 20-cm rain and snow gauge, which was located at the field camp (Fig. 1).

Water transparency was measured with a standard 22-cm Secchi disk. A bathythermograph (BT) was used to obtain temperature–depth profiles. Surface temperature for BT calibration was measured with a standard bucket thermometer. Methods used to estimate lake water residence time have been described in detail by Stockner et al. (1980).

Water samples were collected from stations in the north and south basins of Mohun Lake at least monthly from 1977 to 1980. Sampling at the Comida basin station was conducted from October 1979 to July 1980.

TABLE 2. Dissolved nitrogen concentrations in representative Mohun streams before forest fertilization.

Stream	Nitrogen species (mg N·L^{-1})	1978		1979								
		Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.
Control 2	Urea	< 0.005	< 0.005	< 0.005	< 0.005	< 0.005	< 0.005	< 0.005	< 0.005	< 0.005	< 0.005	< 0.005
	$NH_4 + NH_3$	< 0.004	< 0.004	< 0.004	< 0.004	< 0.004	< 0.004	< 0.004	< 0.004	< 0.004	< 0.004	< 0.004
	NO_3	0.001	0.001	0.001	0.007	0.027	0.016	0.004	0.023	0.018	0.010	0.001
Type I	Urea	< 0.005	< 0.005	< 0.005	< 0.005	< 0.005	< 0.005	< 0.005	< 0.005	< 0.005	< 0.005	< 0.005
	$NH_4 + NH_3$	< 0.004	< 0.004	< 0.004	< 0.004	< 0.004	< 0.004	< 0.004	< 0.004	< 0.004	< 0.004	< 0.004
	NO_3	0.001	0.001	0.001	0.002	0.002	0.001	0.004	0.006	0.004	0.003	0.001
Type II	Urea	< 0.005	< 0.007	< 0.005	< 0.005	< 0.005	< 0.005	< 0.005	< 0.005	< 0.005	< 0.005	< 0.005
	$NH_4 + NH_3$	< 0.004	< 0.007	< 0.004	< 0.004	< 0.004	< 0.004	< 0.004	< 0.004	< 0.004	< 0.004	< 0.004
	NO_3	< 0.001	0.011	0.040	0.025	0.010	0.006	0.058	0.042	0.040	0.018	0.001

A 3-L Van Dorn bottle was used to take water samples from depths of 1, 3, 5, and 20 m. A 2-L plastic bottle was filled from each sampling depth and transported to the laboratory in a light-tight cooler.

Lake water samples were analyzed at the Pacific Biological Station, Nanaimo, B.C. Total alkalinity was determined using the standard potentiometric method (APHA 1976). Total phosphorus, nitrate, and soluble reactive silicon were analyzed according to the methods of Stephens and Brandstaetter (1983). Particulate nitrogen was determined in a Perkin-Elmer model 240 CHN analyzer.

Samples for chlorophyll determinations were collected in 1-L polyethylene bottles from depths of 1, 3, 5, and 20 m and filtered onto Millipore HA filters (47-mm diameter, 0.8-μm pore size) at a vacuum pressure not exceeding 20 cmHg. After filtration, samples were frozen at −5°C. At the time of analysis, filters were macerated in 90% acetone and the filtrate was analyzed in a Turner model III fluorometer using the methods of Strickland and Parsons (1972).

Lugol's acetate-preserved phytoplankton samples were counted and identified using a Wild M40 inverted microscope and Utermöhl's (1958) settling method. Cell numbers were converted to volumes using values calculated by Stockner and Armstrong (1971) and Stockner and Shortreed (1975).

Results and Discussion

Stream Conditions before Forest Fertilization

In all streams during the year prior to fertilization, DN was dominated by nitrate. Ammonia and urea concentrations generally remained at undetectable levels (Table 2). These data are similar to those reported in other coastal streams of British Columbia (Ward and Slaney 1979; Scrivener 1975; Feller and Kimmins 1979). The relationship of nitrate and ammonia concentrations to discharge has been found to be statistically insignificant by Feller and Kimmins (1979) and highly variable by Scrivener (1975). This suggests that there is random variation in dissolved nitrogen concentrations at varying stream flows. Assuming this relationship to be true for Mohun streams, direct comparisons of nitrogen transport between streams using concentration data are possible even when stream discharges are different.

Heavy rainfall and cool temperatures prevailed during late fall and winter of 1979 (Fig. 2 and 3). In January 1980, snow accumulated and large areas of Mohun Lake froze. During this

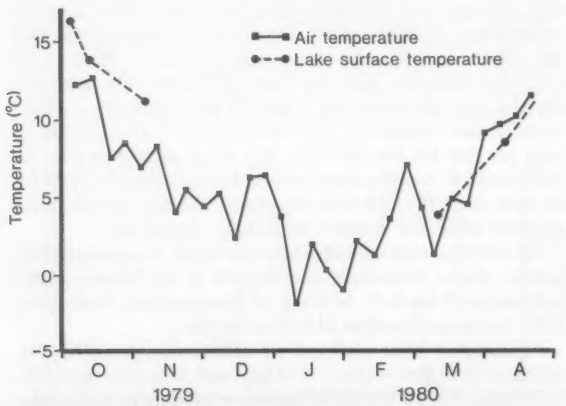


FIG. 3. Mean weekly air and lake surface temperatures in study area.

TABLE 3. Overlap of fertilizer (kg urea·ha^{-1}) into leave (unfertilized) strips bordering streams and lakeshore. Relative differences between computer and visual guidance methods are shown. Number in parentheses refer to ±1 SD.

Location	Distance from stream or lakeshore (m)									
	10	20	30	40	50[a]	60	70	80	90	100
Lower Crescent Creek south side (computer guidance)	0	1.0 (0.9)	2.0 (1.5)	3.0 (2.5)	4.0 (3.2)	16 (12.1)	97 (42)	220 (131)	270 (210)	380 (245)
Mohun South lakeshore (computer guidance)	0	3.0 (2.1)	9.0 (4.8)	20 (11.4)	43 (22)	43 (31)	40 (27)	130 (62)	250 (141)	350 (212)
Lower Crescent Creek north side (visual guidance)	0	0	0	0	0.5 (0.3)	0.9 (0.6)	1.7 (0.8)	2.5 (1.4)	5.8 (2.4)	22.3 (14.8)

[a]The 50-m location is the leave strip boundary.

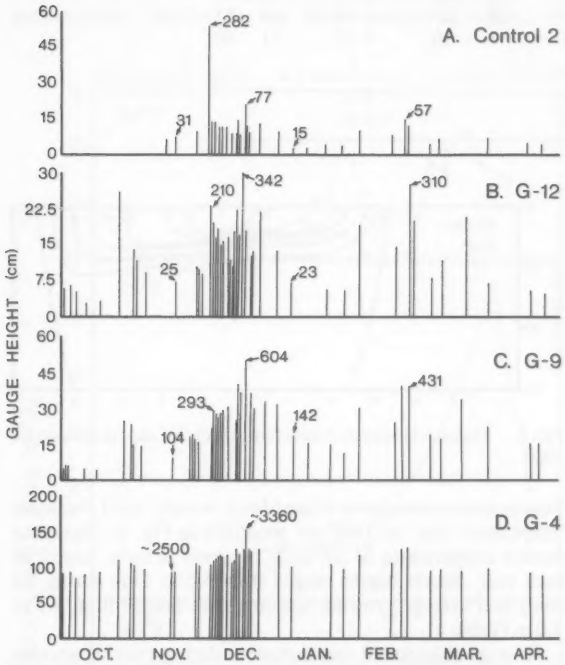


FIG. 4. Daily stream gauge heights at four locations in study area. Assigned values refer to spot flow measurements (L·s^{-1}).

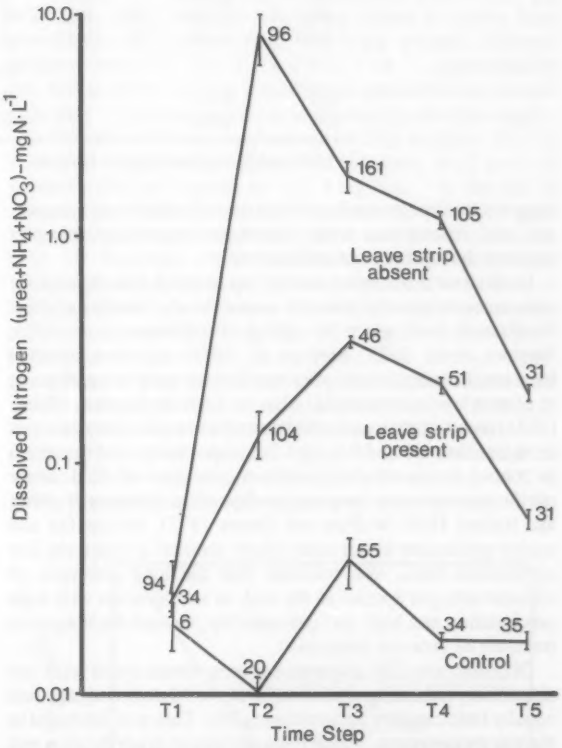


FIG. 5. Interactions of leave strip and time for dissolved nitrogen concentrations in Mohun drainage streams after forest fertilization with urea. Each point shown is a mean accompanied by 95% confidence limits and the respective sample size.

period stream temperatures were 1–2°C in all drainages. In February, lake ice melted and precipitation decreased.

Stream discharges throughout the period fluctuated widely in response to precipitation changes (Fig. 4). This rapid hydrologic flux is typical of coastal streams (Feller 1975; Feller and Kimmins 1979; Scrivener 1975) and is due to high permeability of the coarse granular soils.

Transport of Nitrogen in Streams after Fertilization

During forest fertilizer applications some overlap into the 50-m leave strips occurred, but in all cases fertilizer loads to leave strips were < 5% of that in treated areas (Table 3). Within 10 m of streams or lake margins, no overlap was apparent.

After fertilization, significant differences (ANOVA, $P < 0.001$) were found in the interaction of treatment condition levels with time (Fig. 5). Dissolved nitrogen concentrations in streams without leave strips peaked within the first day after treatment and were two orders of magnitude greater than control concentrations (Table 4). The high concentrations of urea and ammonia are attributed to the direct introduction of fertilizer to watercourses. Peak DN concentrations in streams with leave strips were one order of magnitude greater than control levels ($P < 0.001$) and occurred about 2 wk after fertilization (Fig. 4). Since ammonia is a nonmobile ion in forest soils (Wollum and Davey 1975), its high concentration in streams with leave strips

TABLE 4. Summary of peak dissolved nitrogen concentrations and times to achieve peak and return to pretreatment levels in each of the monitored streams. A, day of peak concentration; B, days required to return to pretreatment concentration.

Stream	Urea peak ($mg\ N \cdot L^{-1}$)	A	B	Ammonia peak ($mg\ N \cdot L^{-1}$)	A	B	Nitrate peak ($mg\ N \cdot L^{-1}$)	A	B
Streams not protected by leave strips									
3	49.3	1	140	3.36	2	109	0.34	40	71
4	8.6	1	143	2.09	19	123	0.31	59	84
5	7.4	1	140	0.53	6	79	0.22	3	12
6	19.5	1	140	4.22	8	97	0.79	34	61
7	32.4	1	141	3.68	7	135	0.22	59	47
11	1.75	1	136	1.13	8	108	0.51	7	26
12	57.6[a]	1	137	4.78	1	83	0.31	14	6
Streams protected by leave strips									
9	0.265	8	144	0.215	16	136	0.19	75	27
10	0.454	7	108	0.472	16	136	0.15	16	4
10a	0.658	8	128	0.243	19	123	0.19	49	51
10b	0.095	7	102	0.195	11	20	0.10	11	10
Control									
C-1	0.02			0.015			0.11		
C-2	0.015			0.010			< 0.02		

[a]Affected by fertilizer spill at heliport.

suggests that ion processing within the soil matrix was minimal, and soil macropores were important as primary transport conduits during heavy rainfall events.

In all streams (except controls), up to 144 d was required for urea concentrations to return to control levels. In other studies, fertilization took place in spring (Fredriksen et al. 1974; Meehan et al. 1975; Stay et al. 1978) and concentration increases in watercourses after fertilization were less and return to control levels more rapid. Also, in a fall application, Moore (1974) reported peak urea nitrogen and ammonia nitrogen levels to be less than 1.5 and 0.2 $mg \cdot L^{-1}$, respectively, and the return to control levels occurred within a maximum of 42 d. Since nitrification rates are temperature dependent (Otchere-Boateng and Ballard 1978; Wollum and Davey 1975), the late fall and winter application in our study likely resulted in relatively low nitrification rates. We conclude that the long residence of reduced nitrogen species in the soil, in combination with high precipitation and high soil permeability, caused the long-term transport of urea and ammonia.

Differences in DN transport between stream types were not significant, indicating that streams of the Mohun drainage had equally little capacity for processing DN. This was attributed to the low temperatures, which reduced rates of denitrification and immobilization (Alexander 1977; Hill 1979; Johnson et al. 1976). In addition, periphyton and other organic matter, which provide substrates for nitrogen processing (Fisher and Likens 1973; McColl 1974; Minshall 1978), were removed from the streams by the frequent freshets, which reduced spiralling rates (Newbold et al. 1981) and further lessened differences between stream types.

Limnology of Mohun Lake

Mohun Lake is an oligotrophic lake typical of many lakes on the British Columbia coast, which generally have high flushing rates, low inorganic nutrient concentrations, and low phytoplankton biomass and productivity (Stockner 1981). The lake is dimictic, and ice cover generally lasts for 1–3 mo each year.

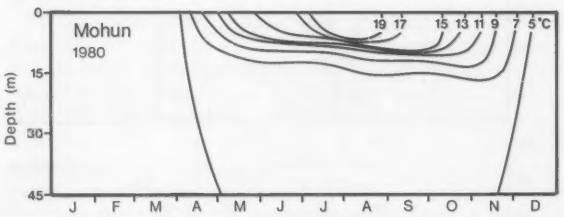


FIG. 6. Seasonal temperature structure in Mohun Lake south basin for 1980.

Stratification commences in late March or early April. Seasonal temperature data for 1980 are presented in Fig. 6. Maximum surface temperatures of 20–23°C occurred in early August of each year. Secchi depths ranged from 5.5 to 11 m during the study and average growing season values ranged from 6.7 to 9.0 m (Table 5).

Average chlorophyll concentrations during growing seasons throughout the study ranged from 0.7 $\mu g \cdot L^{-1}$ in 1977 to 2.23 $\mu g \cdot L^{-1}$ in 1980 (Fig. 7). Highest concentrations occurred during October in three of the four study years. Spring concentrations of chlorophyll also increased in each successive year of the study, suggesting that effects of enrichment with nitrogen and phosphorus during the lake fertilization program were to some extent cumulative. Carlson (1977) has shown that Secchi depth–chlorophyll relationships can be useful indicators of trophic status and predictors of algal biomass when the light attenuation by nonalgal substances in a lake is constant and/or low. In Mohun Lake, changes in Secchi depth at low concentrations of chlorophyll ($< 5\ \mu g \cdot L^{-1}$) were highly correlated, suggesting that attenuation of light from allochthonous material was insignificant (Lorenzen 1980) (Fig. 8). This is a further indication of the ultra-oligotrophic nature of Mohun Lake throughout the 4-yr study.

Spring overturn total phosphorus concentrations were 4–5 $\mu g \cdot L^{-1}$ throughout the study. From 1977 to 1979 the phos-

TABLE 5. Average values of limnological characteristics of Mohun Lake during the growing season. Data are from the south basin.

	1977	1978	1979	1980
Surface temperature (°C)	16.5	15.3	17.7	15.5
Mixed layer depth (m)	8.7	11.1	7.9	8.5
Secchi depth (m)	9.0	7.4	8.4	6.7
Soluble reactive silicon (mg $Si \cdot L^{-1}$)	1.05	0.64	0.42	0.63
Nitrate ($\mu g\ N \cdot L^{-1}$	2.9	6.0	5.1	19.8
Total phosphorus ($\mu g\ P \cdot L^{-1}$)	2.2	5.0	6.3	2.0
Phosphorus load (mg $P \cdot m^{-2} \cdot wk^{-1}$)	2.1	2.2	1.4	0
Chlorophyll ($\mu g \cdot L^{-1}$)	0.89	1.75	1.23	2.23
Total algal volume ($mm^3 \cdot m^{-3}$)	484	1012	1048	2247

phorus load from fertilizer ranged from 0.18 to 0.25 $\mu g\ P \cdot L^{-1} \cdot wk^{-1}$. By comparison, Schindler et al. (1971) utilized a phosphorus load 50 times higher in the experimental fertilization of Lake 227 in the Experimental Lakes Area (ELA) in northwestern Ontario. In our study, treatment resulted in average epilimnetic total phosphorus concentrations increasing from 2.2 $\mu g \cdot L^{-1}$ in the first year of lake fertilization (1977) to 5.4 $\mu g \cdot L^{-1}$ in 1979. In 1980, the average was 1.9 $\mu g \cdot L^{-1}$.

From 1977 to 1979 nitrate concentrations were 15–25 $\mu g\ N \cdot L^{-1}$ at spring overturn and spring nitrate to spring total phosphorus ratios ranged from 3 to 6 (by weight). Nitrogen additions were low (0.8–1.1 $\mu g\ N \cdot L^{-1} \cdot wk^{-1}$, approximately one half as nitrate and the remainder as ammonia) and did not constitute substantial increases to the spring nitrogen supply. The N:P ratio of the fertilizer was only 4.5 by weight or 10:1 on an atomic weight basis. Nitrate concentrations in all years of treatment declined rapidly to < 1–3 $\mu g\ N \cdot L^{-1}$ by the end of May and remained near the detection limit of 1 $\mu g\ N \cdot L^{-1}$ until fall overturn in October or November in each of the lake basins (Fig. 9). Schindler (1977) and Barica (1975) reported that nitrogen-fixing cyanophytes became dominant in the summer or fall phytoplankton community when either added or incipient nutrient concentrations reached an N:P ratio of < 5 (by weight). However, nitrogen-fixing cyanophytes also have a higher phosphorus requirement than most other phytoplankton, and before nitrogen fixation commences the phosphorus supply must exceed a required threshold (Doremus 1982). In our study, despite the very low summer nitrate concentrations and the addition of nutrients at a low fertilizer N:P ratio from 1977 to 1979, cyanophytes formed only a very minor portion of the

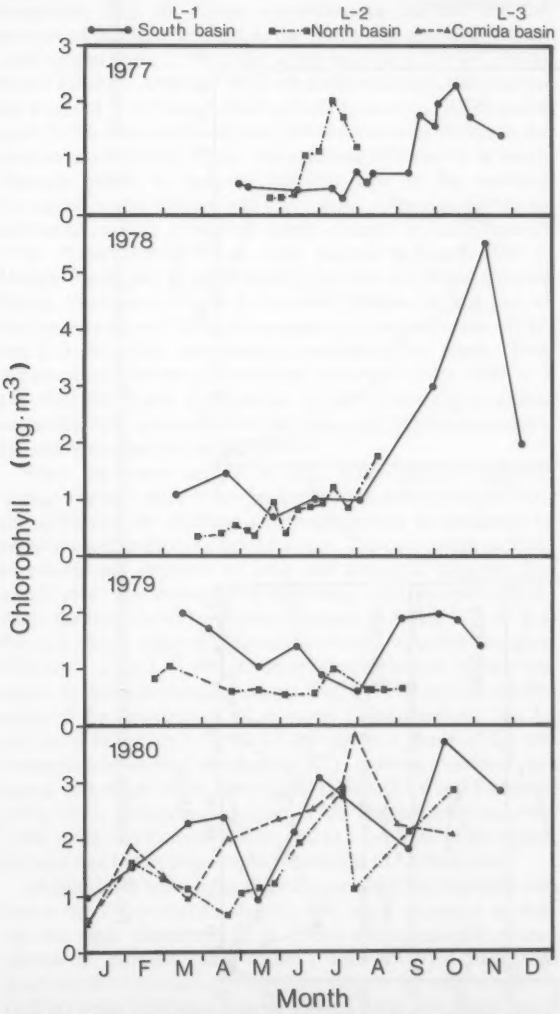


FIG. 7. Variation in mean epilimnetic chlorophyll concentrations in Mohun Lake during 1977–80.

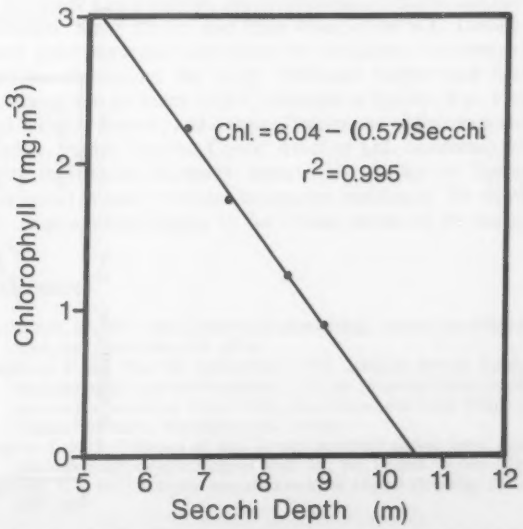


FIG. 8. Chlorophyll–Secchi depth relationship in Mohun Lake.

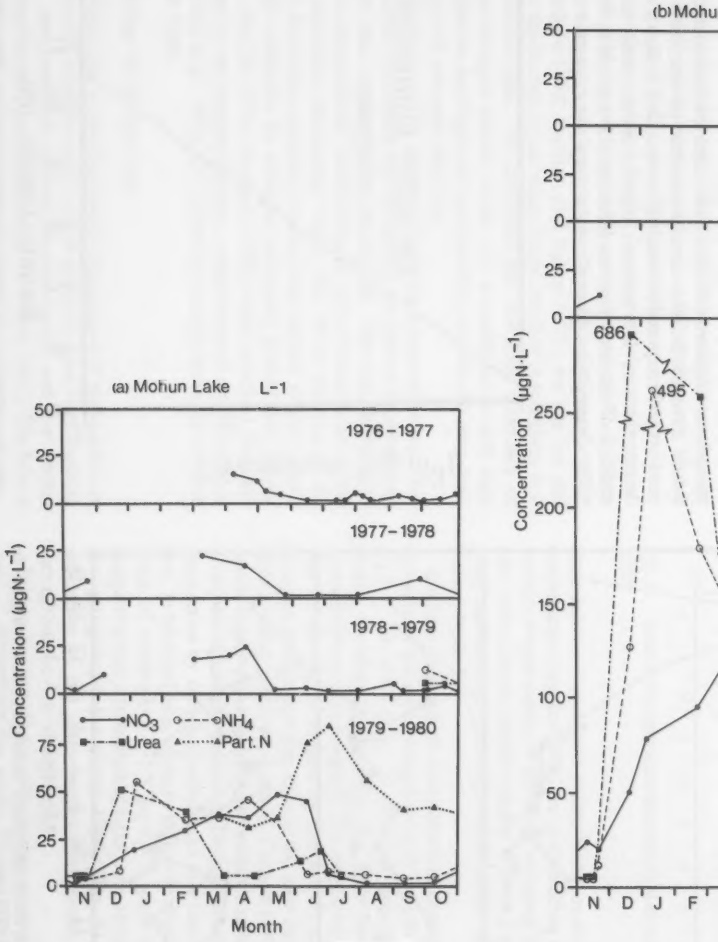
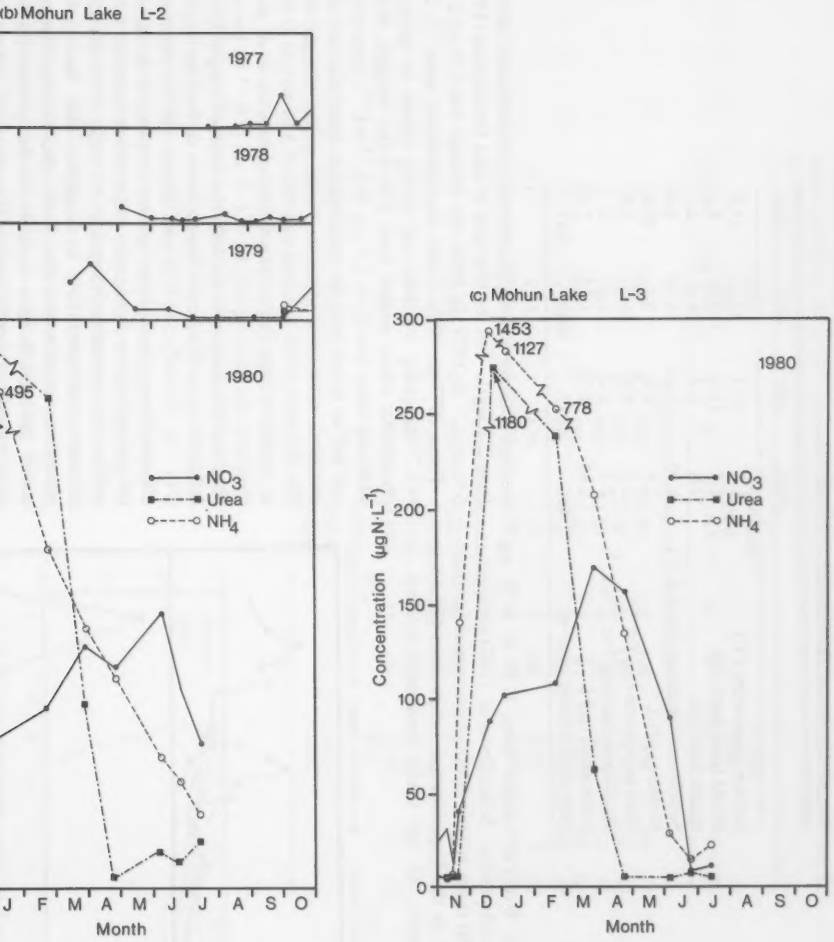


FIG. 9. Variation in mean dissolved nitrogen concentrations in Mohun La



Mohun Lake during 1977–80 in the (a) south basin, (b) north basin, and (c) Comida basin.

TABLE 6. Estimates of fertilizer nitrogen loading at time of peak concentrations in Mohun Lake basins and minimum percent loss of fertilizer from drainages.

	Mohun south	Mohun north	Comida basin
Date of peak concentration	Feb. 20, 1980	Dec. 18, 1979	Dec. 18, 1979
Peak increase in lake basin N (kg)	4 535	5 189	4 503
% loading increase over pretreatment level	55	547	1 924
Lake basin volume (m^3)	7.9×10^7	8.2×10^6	1.7×10^6
Drainage area fertilized (ha)	1 065[a]	503	996
Amount of fertilizer applied (kg N)	213 000[a]	100 680	199 200
% loss from drainage basin (minimum estimate)	2.1[a]	5.2	2.3

[a]Sum of Mohun south and Crescent drainage basins.

summer phytoplankton community. In Mohun Lake, we suggest that while N:P ratios prior to forest fertilization favored nitrogen fixers, phosphorus supply was well below the threshold required for fixation to commence.

Within 1 mo after forest fertilization, DN concentrations were three orders of magnitude greater than prefertilization concentrations in the north and Comida basins, while in the south basin, concentrations increased by only one order of magnitude (Fig. 9). These concentrations indicate that the amount of fertilizer applied to the forest and reaching Mohun Lake ranged from 2.1% in the south basin to 5.2% in Comida basin (Table 6). Although these are underestimates, they exceed the losses of < 0.5% reported by Fredriksen et al. (1974) and of up to 2–3% reported by Moore (1974) for several studies in the northwestern United States. We attribute differences in losses between basins to reduced fertilizer loss in the southern drainages, where streams had leave strips. Urea concentrations decreased steadily after peak levels occurred in early January 1980. Prefertilization levels were reached in March 1980 in Mohun South and in April 1980 in Mohun North and Comida basins. Ammonia followed a similar pattern, but the rate of decline was slower. Minimum ammonia concentrations occurred 2–3 mo after urea reached prefertilization levels. Peak nitrate concentrations did not occur until April–June 1980, 5–7 mo after the forest fertilization. A rapid decrease in nitrate concentrations occurred after the peak, and minimum concentrations were reached by July 1980.

Since the major decline in urea concentrations occurred during winter, a time of low phytoplankton production and high precipitation, we attribute its disappearance to oxidation to ammonia and to flushing from the lake. The concurrent increase of nitrate and decrease of urea and ammonia suggests that nitrification was important in regulating nitrogen species flux. Also, the increase of particulate nitrogen (0.88 $\mu g \cdot L^{-1} \cdot d^{-1}$) at the time (May–July) of declining ammonia and nitrate concentrations (1.2 $\mu g \cdot L^{-1} \cdot d^{-1}$) indicates that biological uptake was active in nitrogen transformations (Fig. 9). The several months required for completion of nitrogen transformations can be attributed to reduced microbial activity as a result of the low winter temperatures (Alexander 1977), reduced oxidation processes as a result of the tannins and lignins (Rice and Pancholy 1972, 1973; Stumm and Morgan 1970), which visibly occurred in the north and Comida basins, and to a low level of biological activity due to the oligotrophic condition of Mohun Lake.

Mohun Lake has a large littoral zone (55% of total lake area above the compensation depth), and large increases in both benthic algae (Shortreed et al. 1984) and submerged macrophytes (R. Sjolund, pers. comm.) were observed during the years of lake fertilization. Therefore, despite the relatively short (1.5 yr) water residence time of Mohun Lake, it is likely that a substantial portion of the nutrient inputs to the lake was bound by benthic flora and later recycled (Fee 1979). These recycling or internal loading processes may have provided a greater phosphorus supply to the lake in 1980 (when no phosphorus fertilizer was added) than was available prior to lake fertilization.

Average algal volume increased from 484 to 1048 $mm^3 \cdot m^{-3}$ in the 3 yr of lake fertilization and was 2247 in 1980, or 2.1 times greater than in 1979, the last year of lake fertilization. Chlorophyll was about 1.8 times greater in 1980 than in 1979. Algal volume increased proportionately more than chlorophyll in 1980 because of increases in the abundance of the diatom *Rhizosolenia* sp. and to a lesser extent *Dinobryon* sp. and *Melosira granulata*, species that have relatively little chlorophyll per unit volume.

We attribute the lack of nitrogen-fixing cyanophytes in Mohun Lake prior to forest fertilization either to an inadequate phosphorus supply (Doremus 1982) or to a lack of an essential element such as Fe (Wurtsbaugh and Horne 1983). After forest fertilization, N:P ratios were high enough to further reduce the possibility of nitrogen fixation occurring in Mohun Lake (Schindler et al. 1971). The low N:P ratio prior to forest fertilization suggests that the lake's phytoplankton community was nitrogen limited for part of each growing season from 1977 to 1979 and that the higher biomass in 1980 occurred as a result of the increased nitrogen supply.

Acknowledgments

We thank Ken Stephens, Pacific Biological Station, and Paul Kluckner, Kerry Taylor, and Peter Wong of the B.C. Government Environmental Laboratory for assistance in chemical analyses throughout the study. Financial support and field assistance was provided by B.C. Ministry of Forests, B.C. Fish and Wildlife Branch, and Canada Department of Fisheries and Oceans, Pacific Region. Conair Aviation Ltd. conducted the forest fertilization treatment. Bruce Nidle drafted the figures and Isabel Warner provided computing assistance. We thank Dr. Eugene Hetherington for his critical review of the manuscript.

References

ALEXANDER, M. 1977. Introduction to soil microbiology. 2nd ed. John Wiley & Sons, Inc., New York, NY. 467 p.

AMERICAN PUBLIC HEALTH ASSOCIATION. 1976. Standard methods for the examination of water and wastewater. 14th ed. American Public Health Association, American Water Works Association, and Water Pollution Control Federation, Washington, DC. 1193 p.

BARICA, J. 1975. Collapses of algal blooms in prairie pothole lakes: their mechanism and ecological impact. Verh. Int. Ver. Limnol. 19: 606–615.

CARLSON, R. E. 1977. A trophic state index for lakes. Limnol. Oceanogr. 22(2): 361–369.

DOREMUS, C. 1982. Geochemical control of dinitrogen fixation in the open ocean. Biol. Oceanogr. 1(4): 429–436.

FEE, E. J. 1979. A relation between lake morphometry and primary productivity and its use in interpreting whole lake eutrophication experiments. Limnol. Oceanogr. 24: 401–406.

FELLER, M. C. 1975. Initial effects of clearcutting on the flow of chemicals through a forest watershed ecosystem. Ph.D. dissertation, University of British Columbia, Vancouver, B.C. 352 p.

FELLER, M. C., AND J. P. KIMMINS. 1979. Chemical characteristics of small streams near Haney in southwestern British Columbia. Water Resour. Res. 15(2): 247–258.

FISHER, S. G., AND G. F. LIKENS. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. Ecol. Monogr. 43(4): 421–439.

FREDRIKSEN, R. L., D. G. MOORE, AND L. A. NORRIS. 1974. Impact of timber harvest, fertilization, and herbicide treatment on streamwater quality in western Oregon and Washington, p. 283–313. *In* B. Bernier and C. W. Wingett [ed.] Soils and forest management. Proc. 4th North American Forest Soils Conference, Quebec, Canada.

HILL, A. R. 1979. Denitrification in the nitrogen budget of a river ecosystem. Nature (London) 281: 291–292.

JOHNSON, A. H., D. R. BOULDIN, E. A. GOYETTE, AND A. M. HEDGES. 1976. Nitrate dynamics in Fall Creek, New York. J. Environ. Qual. 5(4): 386–391.

KLUCKNER, P. D., K. D. TAYLOR, AND P. P. M. WONG. 1980. Automated determination of urea in freshwater samples. B.C. Ministry of Environment, project No. P9022. 16 p.

LE BRASSEUR, R. L., C. D. MCALLISTER, W. E. BARRACLOUGH, O. D. KENNEDY, J. MANZER, D. ROBINSON, AND K. STEPHENS. 1978. Enhancement of sockeye salmon (*Oncorhynchus nerka*) by lake fertilization in Great Central Lake: summary report. J. Fish. Res. Board Can. 35: 1580–1596.

LORENZEN, M. W. 1980. Use of chlorophyll–Secchi disk relationships. Limnol. Oceanogr. 25(2): 371–372.

MCCOLL, R. H. S. 1974. Self-purification of small freshwater streams: phosphate, nitrate and ammonium removal. N. Z. J. Mar. Freshw. Res. 8(2): 375–388.

MEEHAN, W. R., R. B. LOTSPEICH, AND E. W. MUELLER. 1975. Effects of forest fertilization on two southeast Alaska streams. J. Environ. Qual. 4(1): 50–55.

MILLER, R. E., D. L. REUKEMA, AND R. L. WILLIAMSON. 1979. Response to fertilization in thinned and unthinned Douglas-fir stands, p. 150–157. *In* S. P. Gessel, R. M. Kenady, and W. A. Atkinson [ed.] Proceedings, forest fertilization conference, Union, WA. Contr. 40, College of Forest Resources, University of Washington, Seattle, WA.

MINSHALL, G. W. 1978. Autotrophy in stream ecosystems. Bioscience 28(12): 767–771.

MOORE, D. G. 1974. Impact of forest fertilization on water quality in the Douglas-fir region — a summary of monitoring studies, p. 209–219. Proc. Natl. Conv. Soc. Am. For., NY. Sept. 22–26, New York.

1975. Effects of forest fertilization with urea on stream water quality — Quilcene Ranger District, Washington. U.S. Dep. Agric. For. Serv. Res. Note PNW-241: 9 p.

NEWBOLD, J. D., J. W. ELWOOD, R. V. O'NEILL, AND W. VAN WINKLE. 1981. Measuring nutrient spiralling in streams. Can. J. Fish. Aquat. Sci. 38: 860–863.

OTCHERE-BOATENG, J., AND T. M. BALLARD. 1978. Urea fertilizer effects on dissolved nutrient concentration in some forest soils. Soil Sci. Soc. Am. J. 42: 503–508.

RICE, E. L., AND S. K. PANCHOLY. 1972. Inhibition of nitrification by climax ecosystems. Am. J. Bot. 59: 1033–1040.

1973. Inhibition of nitrification by climax ecosystems. II. Additional evidence and possible role of tannins. Am. J. Bot. 60: 691–702.

SAFFORD, L. O., AND S. M. FILIP. 1974. Biomass and nutrient content of four year old fertilized and unfertilized northern hardwood stands. Can. J. For. Res. 4: 549–554.

SCHINDLER, D. W. 1977. Evolution of phosphorus limitation in lakes. Science (Washington, DC) 195: 260–262.

SCHINDLER, D. W., F. A. J. ARMSTRONG, S. K. HOLMGREN, AND G. J. BRUNSKILL. 1971. Eutrophication of lake 227, Experimental Lakes Area, northwestern Ontario, by addition of phosphate and nitrate. J. Fish. Res. Board Can. 28: 1763–1782.

SCRIVENER, J. C. 1975. Water, water chemistry and hydrochemical balance of dissolved ions in Carnation Creek watershed, Vancouver Island, July 1971–May 1974. Fish. Mar. Serv. Tech. Rep. 564: 141 p.

SHORTREED, K. S., A. C. COSTELLA, AND J. G. STOCKNER. 1984. Periphyton biomass and species composition in 21 British Columbia lakes: seasonal abundance and response to whole-lake nutrient additions. Can. J. Bot. 62 (In press)

STAY, E. S., K. W. MALUEG, R. E. AUSTIN, M. R. CROUSE, A. KATKO, AND S. E. DOMINGUEZ. 1978. Ecological effects of forest fertilization with urea on small Western Cascade streams of Oregon, U.S.A. Verh. Int. Ver. Limnol. 20: 1347–1358.

STEPHENS, K., AND R. BRANDSTAETTER. 1983. A laboratory manual: collected methods for the analysis of water. Can. Tech. Rep. Fish. Aquat. Sci. 1159: 68 p.

STOCKNER, J. G. 1981. Whole-lake fertilization for the enhancement of sockeye salmon (*Oncorhynchus nerka*) in British Columbia, Canada. Verh. Int. Ver. Limnol. 21: 293–299.

STOCKNER, J. G., AND F. A. J. ARMSTRONG. 1971. Periphyton of the Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Board Can. 28: 215–229.

STOCKNER, J. G., AND K. S. SHORTREED. 1975. Phytoplankton succession and primary production in Babine Lake, British Columbia. J. Fish. Res. Board Can. 32: 2413–2427.

STOCKNER, J. G., K. S. SHORTREED, AND K. STEPHENS. 1980. The British Columbia Lake Fertilization Program: limnological results from the first 2 years of nutrient enrichment. Can. Tech. Rep. Fish. Aquat. Sci. 924: 91 p.

STRICKLAND, J. D. H., AND T. R. PARSONS. 1972. A practical handbook of seawater analysis. Bull. Fish. Res. Board Can. 67: 311 p.

STUMM, W., AND J. J. MORGAN. 1970. Aquatic chemistry. An introduction emphasizing chemical equilibria in natural waters. wiley-Interscience, New York, NY. 538 p.

TARRANT, R. F., AND R. R. SILEN. 1966. Growth and nutrient uptake of irrigated young Ponderosa pine after fertilizer treatment. Soil Sci. Am. Proc. 30(6): 796–799.

TRAVERSY, W. J. 1971. Methods for chemical analysis of waters and wastewaters. Water Quality Division, Inland Waters Branch, Dep. Fish. and For., Ottawa, Ont. 169 p.

UTERMÖHL, H. 1958. Zur Vervollkommung der Qualitativen Phytoplankton-Methodik. Mitt. Int. Ver. Limnol. 9: 1–38.

WARD, B. R., AND P. A. SLANEY. 1979. Evaluation of in-stream enhancement structures for the production of juvenile steelhead trout and coho salmon in the Keogh River: Progress 1977 and 1978. Fish. Tech. Circ. No. 45. B.C. Ministry of Environment. 47 p.

WOLLUM, A. G. II, AND C. B. DAVEY. 1975. Nitrogen accumulation, transformation, and transport in forest soils, p. 67–106. *In* B. Bernier and C. H. Winget [ed.] Forest soils and forest land management. Les Presses de L'Université Laval, Quebec, Que.

WURTSBAUGH, W. A., AND A. J. HORNE. 1983. Iron in eutrophic Clear Lake, California: its importance for algal nitrogen fixation and growth. Can. J. Fish. Aquat. Sci. 40: 1419–1429.

Deposition of Fine and Coarse Sand in an Open-Work Gravel Bed

Paul A. Carling

Freshwater Biological Association, The Ferry House, Far Sawrey, Ambleside, Cumbria, England, LA22 0LP

Carling, P. A. 1984. Deposition of fine and coarse sand in an open-work gravel bed. Can. J. Fish. Aquat. Sci. 41: 263–270.

The siltation of an experimental gravel bed, with three grades of sands moving in suspension and as bedload, was examined in a flume. For low suspended sediment concentrations (< 300 mg·L^{-1}) the mean deposition rate was 1.34% of the initial gravel volume filled per hour. Deposition rates for sands 0.15–1.4 mm in diameter with suspended sediment concentrations of 38–9110 mg·L^{-1} and Froude numbers in the range 0.008–1.21 were constant with respect to Froude number. For all concentrations the deposition rate was strongly linearly correlated with the suspended sediment concentration. The downstream decrease in siltation rate from a point source was a negative exponential function of distance from that source. Turbulent resuspension of sediment prevented deposition in a surface layer of gravel of thickness approximately equal to the mean grain size of the gravel. Mean flow data, especially where derived from velocity profile data measured in the outer boundary layer, have limited value for siltation investigations concerned with processes occurring very close to the bed. Practically, results indicate that open-work gravels will rapidly become silted in flows with low concentrations of suspended solids. Consequently, mechanical cleansing of spawning beds has limited value where sediment pollution is likely to be a recurrent problem. A simple equation describing the downstream extent of silting from a point pollution source is presented that requires verification in natural streams.

L'envasement d'un lit de gravier expérimental, comportant trois catégories de sable se déplaçant en suspension et servant de charge de fond, a été étudiée dans un bassin d'essai. Pour les faibles concentrations de sédiments en suspension (< 300 mg·L^{-1}) le taux de dépôt moyen a été de 1,34 % du volume initial de gravier rempli par heure. Les taux de dépôt, pour les sables d'un diamètre de 0,15 à 1,4 mm avec des concentrations de sédiments en suspension variant de 38 à 9110 mg·L^{-1} et des nombres de Froude variant de 0,008 à 1,21, ont été constants par rapport au nombre de Froude. Pour toutes les concentrations, le taux de dépôt était fortement corrélé linéairement avec la concentration des sédiments en suspension. La diminution en aval du taux d'envasement à partir d'une source ponctuelle était une fonction exponentielle négative de la distance depuis cette source. La remise en suspension turbulente de sédiments a empêché le dépôt dans une couche superficielle de gravier d'une épaisseur à peu près égale à la grosseur moyenne des grains du gravier. Les données sur le débit moyen, surtout quand elles sont tirées des profils de vitesse mesurés dans la couche limite supérieure, ont une valeur limitée pour les recherches sur l'envasement axées sur les processus se produisant très près du lit. De façon pratique, les résultats indiquent que les graviers à larges interstices deviendront rapidement envasés dans les écoulements contenant de faibles concentrations de solides en suspension. Par conséquent, le nettoyage mécanique des frayères a une valeur limitée là où la pollution par les sédiments risque d'être un problème périodique. On présente une simple équation décrivant l'importance de l'envasement en aval à partir d'une source ponctuelle de pollution, qui exige une vérification dans les cours d'eau naturels.

Received April 13, 1983
Accepted October 18, 1983

Reçu le 13 avril 1983
Accepté le 18 octobre 1983

The silting of gravel beds is of concern to fisheries biologists. Many investigators have shown that accumulation of fine inorganic fractions (< 1 mm) in the interstices of gravel beds has a detrimental effect on stream biota (Iwamoto et al. 1978).

In North America the bulk of siltation literature refers to the effect of forest management practices that are not conducive to soil conservation. Investigators have sought ways to ameliorate problems of sedimentation in streams after identifying the multivariate processes involved in fine sediment production (e.g. Adams and Beschta 1980).

Potential problems also exist in the United Kingdom. Large areas of upland Britain afforested in the first half of this century will be cleared and replanted by the turn of the century. Present forest management has already been shown to result in sediment problems (Newson 1980) whilst the extensive practice of deep ploughing for drainage increases sediment production, at least in the short term (Robinson 1980). Examples of the effect of inert-sediment pollution on river biota (Herbert et al. 1961; Nuttall 1972; Turnpenny and Williams 1980) and upland channel morphology (Richards 1979) emphasize that appreciable siltation occurs in British rivers, related not only to forestry but also to mining or construction.

Natural siltation in United Kingdom upland water courses shows a seasonal pattern in the amount and spatial distribution of deposition (Smith 1980). Furthermore, the grain size of material settling onto the gravel surface, from low concentration suspensions during base flow, is similar to the material infilling void space in the gravel (Carling and Reader 1982). However, little is presently known of the mechanisms and rates of interchange of sediment from suspension to the interstitial environment (Einstein 1968; Beschta and Jackson 1979). Some

knowledge of processes, rates, and downstream extent of siltation would be invaluable when evaluating pollution impact or gravel restoration programs (Wolman and Schick 1967; Anonymous 1981).

In this paper the deposition of coarse and fine sands in an experimental gravel bed is examined. The importance of the shear stress, water depth, particle size, Froude number, particle Reynolds number, and suspended sediment concentration in relation to siltation rates was considered.

Natural stream bed sediments may be poorly sorted and heavily silted. However, a low silt content is generally regarded as important in the survival of the young stages of salmonids (Iwamoto et al. 1978). Where naturally clean gravel beds do not occur, artificial gravel beds or mechanically cleansed natural gravels have been used to maximize recruitment. The present experiments were designed to pertain particularly to these idealized situations and possibly to natural gravels flushed by floods in shallow upland streams. Further research is required to examine silting in poorly graded bed sediments.

Materials and Methods

A description of the notation used is given in the appendix.

Twenty-five uniform flow experiments were conducted in flumes of rectangular section with smooth sidewalls (Table 1). Clean rounded quartz-density (2.65 $g \cdot cm^{-3}$) gravel (Fig. 1) was used in each test run. The surface was tamped to provide a uniform bed of porosity ~ 0.39.

Experiments were scaled to give Froude numbers from 0.005 to 1.2. The downstream change in concentration of suspended sediment, as settling occurs, may be expected to be a function of V_s/U_* (Camp 1943). All runs were within Owen's (1969) transitional range $0.005 < V_s/U_* < 5.0$, so that the settling rate might be expected to be dependent both on the level of turbulence and the grain size of the suspended sediment.

Fine quartz-density sediment (Fig. 1) was fed into the upstream end of the test section at the water surface using a calibrated sediment feed hopper. Each grade of sand used had a narrow size range (Fig. 1). Initial sediment concentrations were calculated from the constant feed rate and fluid discharge. Owing to problems in manipulating the sediment feed rate it was necessary in the first 16 runs to achieve low concentrations by increasing the fluid discharge rather than reducing the feed rate. As a result, concentrations were a weak inverse function of current speed. During the additional nine runs it was possible to vary the feed rate so that initial concentrations were not dependent on current speed. No suspended sediment profiles were measured, and runs were terminated when the gravel bed was nearly fully silted.

The distribution of sediment through the length of the section was measured using a row of gravel-filled pots buried with the tops flush with the gravel surface down the centre of the flume. In addition, a row of pots across the flume recorded lateral variation in siltation.

Pots in runs 17–25 were made larger than in runs 1–16 and were also permeable, nine 1-cm-diameter holes having been drilled in each side and the base. Deposited sand was prevented from escaping by 0.063-mm mesh glued over the holes.

All fine sediment transported out of the flume was entrapped in a fine-mesh bag (0.063-mm aperture). Average siltation rates could be calculated from the difference between the input and output of sand, as well as from the quantity of sand deposited in the siltation pots.

TABLE 1. Details of experimental materials.

	Grassholme flume (runs 1–16)	Keele flume (runs 17–25)
Water recirculated	No	Yes
Sediment recirculated	No	No
Max. discharge ($L \cdot s^{-1}$)	117.0	103.0
Width (m)	0.98	0.81
Length (m)	12.0	12.8
Working section (m)	6.0	6.0
Gradient	0.014 (fixed)	Variable
Gravel depth (m)	0.15	0.10
Sediment concentration ($mg \cdot L^{-1}$)	42–263	311–9045
Run time (min)	60–120	1.5–18
No. of downstream pots	10	6
Lateral pots	4	4
Pot volume (cm^3)	355	2111
Pot depth (cm)	8.4	10.0
Pot surface area (cm^2)	32.0	266.0
Pot spacing (m)	0.5	1.0

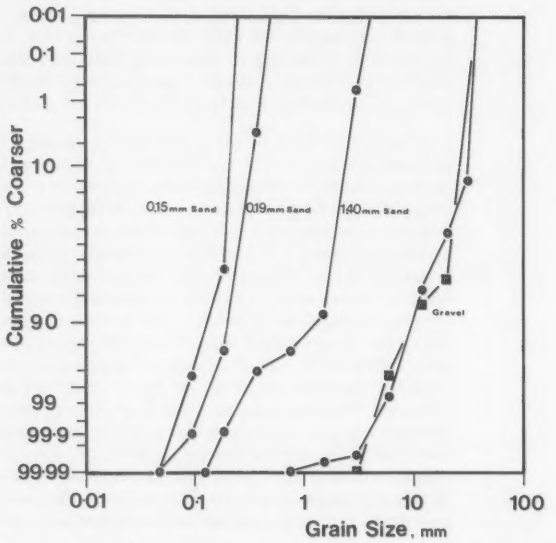


FIG. 1. Cumulative frequency curves of sediment grain sizes used in sand infiltration experiments. ●, gravel runs 1–16; ■, gravel runs 17–25.

Water surface slope was measured using a manometer or point gauge. Current speed was measured at 0.6 of the depth at 9-cm intervals across the width at the upstream end of the test section using an Ott current meter. Depth was measured at 9-cm intervals using a point gauge at the entrance and exit sections. During runs 1–16, at midstream 2 m down the section, a velocity profile was measured at 0.5- or 1.0-cm increments above the bed with the lowest measure 2.5 cm above the bed.

The shear velocity was calculated from logarithmic velocity profiles assuming that a value for von Kármán's constant of 0.40 is valid for velocity profiles with suspended sediment (Coleman 1981):

$$(1)\quad \bar{U}_z = \frac{U_*}{0.40} \ln \frac{Z}{z_0}.$$

No velocity profiles were taken in runs 17–25; consequently, in

these latter runs the shear velocity was calculated from

(2) $S_e = \rho U_*^2/\gamma R$

and related to the shear stress by

(3) $U_* = \sqrt{\tau_0/\rho}$.

Bed roughness was initially estimated using Nikuradse's equivalent sand grain roughness (Schlichting 1968):

(4) $K_s = 30z_0$

but these data could not be related satisfactorily to the grain size of the bed material. Meland and Norrman's (1969) equation for flow over rhombohedrally packed glass beads,

(5) $\log z_0 = 1.951 \log K_s - 0.939$,

gave equivalent roughness values with a mean value of K_s close to the mean grain size of the bed material, i.e. $\bar{K}_s = 1.1\bar{d}$. The result of the present investigation, i.e. $K_s = 0.65d_{50}$ (runs 1–16) and $K_s = 0.44d_{50}$ (runs 17–25), is similar to that of Zagni and Smith (1976) for porous beds composed of single-sized 11- or 17-mm-diameter spheres.

Results

General Observations

For Froude numbers between 0.11 and 0.73 the two fine grades of sand were transported in suspension and in traction, although the proportion moving as bedload decreased at high Froude numbers. Bedload was distinctly pulsatory, possibly associated with "bursting" phenomena close to the bed (Grass 1971), and there was frequent exchange of material between the bedload and the suspended load.

For Froude numbers less than 0.11, fine sand was transported as bedload only. For example, during run 2 as soon as the gravel was fully silted, the bedload formed a carapace of rippled sand with ripple heights of 26 mm and wavelengths in the range 48–90 mm.

During flows characterized by a suspension load, fine sand was introduced into the gravel void space by turbulent pulses as well as gravitational settling. Fine sand deposited at the base of the gravel and thereafter filled the void space at a constant rate leaving only a surface layer, approximately 15 mm thick free of sand. Turbulence resuspended sand from this layer and effectively prevented siltation at the surface, indicating that permanent deposition occurred only below a "zero" velocity plane approximately one pebble diameter below the surface that corresponds to $1.42\bar{K}_s$ or $4.76z_0$.

At Froude numbers greater than 0.70 no bedload transport occurred; grains moved in suspension but were continually entrapped in the surface void space and deposited in the bed.

Only three runs used the coarse sand (Table 2). This material moved solely as bedload and infiltrated the gravel bed unevenly, leaving frequent isolated areas of residual open void space.

Velocity Profiles

Siltation rate is dependent, at least in part, on the turbulent exchange rate at the sediment–water interface (Einstein 1968; McCave 1970). The relative roughness may be expected to influence the degree of turbulence over a rough boundary, turbulence intensity decreasing at low Reynolds numbers and at large values of the relative depth (Nowell 1978). As a result the influence of relative roughness on the velocity profile was examined.

Equation 1 may also be expressed as

(6) $\frac{\bar{U}_z}{U_*} = \frac{1}{\kappa} \ln \frac{Z}{K_s} + C.$

A typical value for the constant C for a rough turbulent planar sandbed is 8.5 (Schlichting 1968). However, C had a smaller value (2.3–4.6) and increased as a function of D/K_s over an experimental bed of 23-mm-diameter hemispheres (Bayazit 1976). Data from the present experiments confirm that a lower value of C may be appropriate for boundaries of gravel; an average value is 4.92. Similarly to Bayazit's results, C also increased with D/K_s (Fig. 2).

Siltation Rate

The mean siltation rate (grams per minute per square metre) was calculated accurately by subtracting the weight of sand caught at the end of the test section from the weight introduced to the test section (Table 2 Δ'_b). Deposition for a constant feed rate (Δ_b) for individual grain sizes varied insignificantly (95% confidence limits on regression slopes) (Draper and Smith 1966, p. 19) with water depth, particle Reynolds number (U_*d/ν), or Froude number ($\bar{U}^2/Dg$). This result contrasts with the deposition rate measured in buried pots (Δ_p) where rates were not only lower but declined, e.g., with Froude number. The latter result, however, was an artifact of the type of pot used in runs 1–16. The average efficiency of the pots in trapping sediment in the first 16 runs was calculated as the ratio between $\bar{\Delta}_p$ and $\bar{\Delta}_b$ (61.9% efficient, $\sigma = 31.6\%$). The reduction in efficiency was most marked for Froude numbers greater than 0.10 (Fig. 3) and may be explained by the absence of intragravel flow, in the solid-walled pots, advecting grains down through the void space. The use of permeable pots in runs 17–25 solved this problem (93.3% efficient, $\sigma = 14.2\%$).

The siltation rate can also be expressed as the percentage of void space filled per hour (Table 2, $\Delta_\%$). The mean rate for runs at low suspended sediment concentrations (runs 1–16) was $1.34\%\cdot h^{-1}$ ($\sigma = 0.08\%\cdot h^{-1}$). The value for runs at high suspended sediment concentrations (runs 17–25) was only slightly higher, $\sim 1.55\%\cdot h^{-1}$. These data are shown in Fig. 4. Also shown are the data of Beschta and Jackson (1979) adjusted to a common scale compatible with the data presented in this paper.

Siltation rates, although not correlated with the hydraulic parameters, were highly correlated with the initial concentration of sand. In runs 1–16, the concentration was a weak inverse function of velocity (see Materials and Methods). Consequently, before plotting the siltation rate as a function of concentration, the rate was divided by the velocity to remove spurious slight curvature in the relationship. The least squares regression equation (significant at the 99.9% level) follows the trend of the data closely (Fig. 5). The constant has the dimensions of a velocity (metres per minute) and represents the average exchange velocity (V'_s) between the flow and the gravel void space. Where unhindered settling occurs, $V'_s = V_s$. Settling was hindered as $V'_s = 10.0\ mm\cdot s^{-1}$ compared with an average value of V_s of $16.7\ mm\cdot s^{-1}$ for the range of fine sands used.

Downstream Siltation Rate

The downstream sorting of sediment is commonly described as an exponential function of distance from the source (e.g.

TABLE 2. Basic data for infiltration experiments. Column 12 is the observed raw deposition rates raw deposition values by the respective feed rate and multiplying by 300.

(1) Run	(2) D (m)	(3) U ($m \cdot s^{-1}$)	(4) Q ($m^3 \cdot s^{-1}$)	(5) F	(6) Z_0 (m)	(7) U_* ($m \cdot s^{-1}$)	(8) K_s (mm)	(9) τ_0 ($N \cdot m^{-2}$)	(10) S_e	(
1	0.113	0.897	0.099	0.726	0.0027	0.115	10.92	13.22	0.0146	
2	0.138	0.364	0.049	0.098	0.0040	0.057	10.22	3.25	0.0030	
3	0.170	0.115	0.019	0.008	0.0040	0.018	14.81	0.32	0.0003	
4	0.137	0.541	0.073	0.218	0.0083	0.115	13.96	13.22	0.0126	
5	0.109	0.838	0.090	0.657	0.0006	0.086	10.55	7.39	0.0084	
6	0.127	0.943	0.117	0.714	0.0016	0.108	11.51	11.66	0.0118	
7	0.103	1.108	0.112	1.215	0.0029	0.212	10.49	44.91	0.0539	
8	0.109	0.942	0.101	0.830	0.0038	0.149	10.86	22.19	0.0252	
9	0.099	0.923	0.090	0.877	0.0022	0.123	10.08	15.12	0.0186	
10	0.125	0.626	0.077	0.320	0.0029	0.087	11.74	7.56	0.0111	
11	0.148	0.357	0.052	0.088	0.0050	0.058	13.64	3.36	0.0030	
12	0.120	0.658	0.077	0.368	0.0023	0.090	11.41	8.09	0.0085	
13	0.106	0.803	0.083	0.620	0.0042	0.136	10.67	18.48	0.0217	
14	0.141	0.381	0.053	0.105	0.0043	0.064	13.30	4.09	0.0038	
15	0.115	0.995	0.112	0.878	0.0048	0.153	11.25	23.39	0.0255	
16	0.109	0.701	0.075	0.460	0.0014	0.080	10.61	6.40	0.0073	
17	0.085	0.431	0.030	0.223	N/D	0.085	8.46	7.22	0.0104	
18	0.072	0.590	0.034	0.491	N/D	0.090	7.77	8.09	0.0135	
19	0.056	0.545	0.025	0.540	N/D	0.078	6.61	6.08	0.0126	
20	0.091	0.687	0.050	0.530	N/D	0.098	9.27	9.60	0.0133	
21	0.120	0.969	0.094	0.800	N/D	0.112	10.88	12.54	0.0138	
22	0.094	1.014	0.077	1.112	N/D	0.126	9.54	15.86	0.0213	
23	0.089	0.980	0.071	1.099	N/D	0.123	9.24	15.12	0.0210	
24	0.120	1.060	0.103	0.954	N/D	0.157	11.15	24.63	0.0210	
25	0.120	1.060	0.103	0.954	N/D	0.157	11.15	24.63	0.0210	

ition rates. Columns 13–15 are values adjusted to a common arbitrary feed rate (300 g·min^{-1}) by dividing

(10) S_e	(11) R (g·min^{-1})	(12) Δ'_b (g·min^{-1}·m^{-2})	(13) Δ_b (g·min^{-1}·m^{-2})	(14) $\Delta_{\%}$ (%·h^{-1})	(15) Δ_p (g·min^{-1}·m^{-2})	(16) d (mm)	(17) C_0 (mg·L^{-1})
.0146	268	26.17	29.30	1.34	12.05	0.1896	45
.0030	268	27.78	31.10	1.42	12.47	0.1896	91
.0003	268	27.67	30.97	1.42	10.04	0.1896	235
.0126	268	24.30	27.20	1.24	36.59	0.1896	61
.0084	268	22.85	25.58	1.17	23.06	0.1896	50
.0118	268	26.83	30.03	1.37	9.98	0.1896	38
.0539	253	25.52	30.26	1.38	14.38	0.1540	38
.0252	253	26.54	31.47	1.44	10.36	0.1540	42
.0186	253	25.46	30.19	1.38	11.94	0.1540	47
.0111	253	24.31	28.83	1.32	14.10	0.1540	55
.0030	253	23.34	27.68	1.27	20.35	0.1540	81
.0085	253	22.84	27.08	1.24	18.66	0.1540	54
.0217	253	23.51	27.88	1.28	16.18	0.1540	51
.0038	529	55.95	31.75	1.45	36.16	1.3963	168
.0255	529	50.16	28.46	1.30	11.10	1.3963	90
.0073	529	53.06	30.10	1.38	28.68	1.3963	111
.0104	3739	—	—	—	45.75	0.1540	1827
.0135	8050	1241.14	46.25	2.12	41.28	0.1540	3900
.0126	4944	764.22	46.37	2.12	34.64	0.1540	3336
.0133	12653	1927.41	45.70	2.09	42.77	0.1540	4184
.0138	6941	951.65	41.13	1.88	32.80	0.1540	1234
.0213	35883	4650.03	38.88	1.78	42.36	0.1540	7757
.0210	38534	5541.57	43.14	1.97	44.47	0.1540	9110
.0210	1924	290.68	45.32	2.07	48.80	0.1540	312
.0210	2806	362.71	38.78	1.77	43.93	0.1540	456

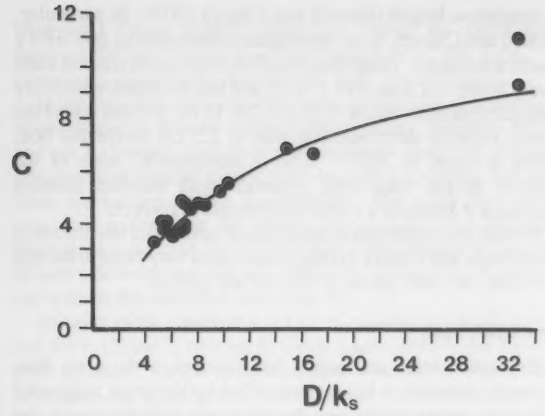


FIG. 2. Coefficient C in equation 6 as a function of D/K_s.

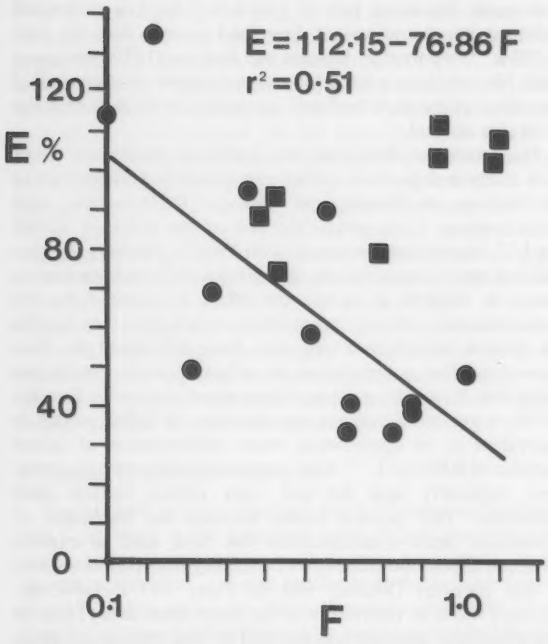


FIG. 3. Efficiency (E) of siltation pots with solid walls, measured as a percentage of siltation in an unconfined gravel bed, decreases as Froude number (F) increases. ● and regression line, runs 1–16; ■, permeable pots (runs 17–25).

Church and Kellerhals 1978; Deigaard 1980). Sundborg (1958) and Stow and Bowen (1980) explained this gradation as a differential transport process based on a sedimentation formula. Sundborg's equation is

$$(7)\quad \Delta' = \frac{V_s p}{D} C_0 e^{-V_s pL/\bar{U}D}$$

where p is 1 minus the ratio between the number of particles entrained and the number deposited at any one location and, expressed as the overall probability of deposition, may be written as V'_s/V_s or $(1 - \tau_0/\tau_t)k$ (McCave and Swift 1976).

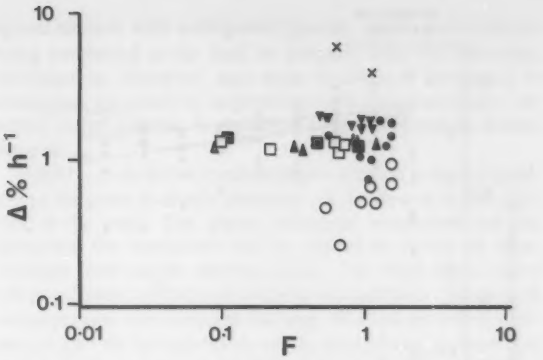


FIG. 4. Siltation rates (Δ%) obtained from pot data, corrected to a common feed rate and plotted as a function of the Froude number (F). Runs 1–16: ▲, 0.15-mm sand; □, 0.19-mm sand; ■, 1.4-mm sand. Runs 17–25: ▼, 0.15-mm sand. Siltation data of Beschta and Jackson (1979): ×, 0.20-mm sand; ●, 0.5-mm sand for low concentrations; ○, 0.5-mm sand for high concentrations.

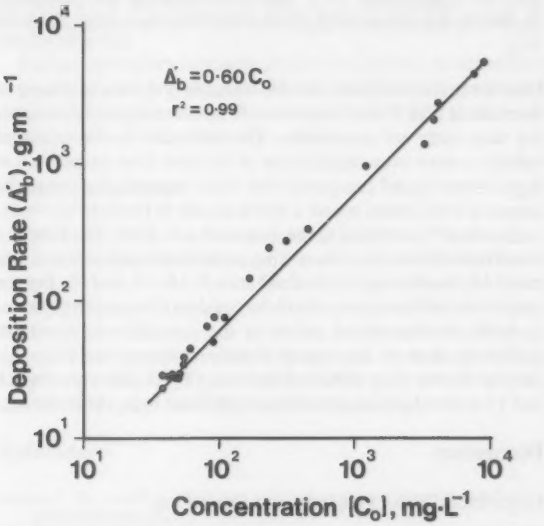


FIG. 5. Relationship of deposition rate (Δ'_b) to the initial concentration of sediment in the fluid (C_0).

Values cannot be greater than 1 and usually are in the range 0.4–1.0 (McCave and Swift 1976).

In the present experiments sand was fed into the channel at the water surface. Consequently, settling grains were transported through a finite distance downstream over the bed before deposition; the distance theoretically is given by

$$(8)\quad L = DUz/V_s.$$

Assuming the proportionality $\epsilon_s/\epsilon = 1$, then $z = V_s/\kappa U_*$. Solution of equation 8 gave L values in a general range of 1–2 m in agreement with observations (Fig. 6).

Deposition rates (Δ_p) for the first metre of experimental section were low and variable and were not included in the following analysis. Despite scatter, the data for runs 1–16 for low sediment concentrations fit the exponential function

$$(9)\quad \Delta_p = 0.2998e^{-0.2211L}.$$

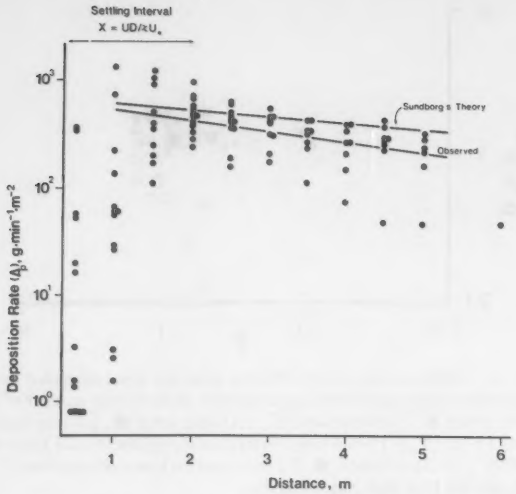


FIG. 6. Experiments 1, 2, and 4–13 showing the exponential decrease in deposition rate (Δ_p) of fine sand from the source suspension (C_0).

Data for individual runs indicate a tendency for the exponent to decrease at high Froude numbers, or as current speed increased, but data were not conclusive. The reduction in the exponent reflects a more even distribution of siltation from suspension at high current speed compared with local deposition close to the source at low current speed: a result similar to Einstein's (1968).

Equation 7 was fitted to the data with $p = 0.60$. The function is not intended to describe sorting by bedload transport and a fit could not be obtained for bedload runs 3, 14, 15, and 16. For the suspended sediment runs the observed data deviate progressively from the theoretical curve in the downstream direction, indicating that p decreased slightly downstream (Fig. 6). Similar results were obtained for runs 17–25 although runs 18 and 19 showed a more pronounced decrease in Δ_p downstream.

Discussion

Logarithmic Velocity Model and Deposition

The lack of correlation of deposition with hydraulic parameters, and with bed shear stress in particular, initially might seem surprising, as observation of particle and tracer motion close to the sediment–water interface indicates that fluid exchange close to the bed is related to the bed shear stress (McCave and Swift 1976). Nevertheless, Einstein (1968) and Lee et al. (1981) concluded that deposition is proportional primarily to the concentration close to the sediment–water interface and that hydraulic controls are of secondary importance.

The logarithmic velocity model, frequently used to obtain mean flow data, is not applicable very close to a rough boundary where flow is complicated owing to separation behind roughness elements. In particular, using outer region observations, the estimation of momentum transfer close to the bed is not possible (Nowell 1978). It follows that if sedimentation is controlled by the hydrodynamics close to, or within, the surface gravel layer (Einstein 1968) then hydrodynamic measures should also be in this layer. The depth of this region is, from studies of depth-limited boundary layers in air and water, of the order of the roughness spacing (Mulhearn and Finnigan 1978) or roughness height (Nowell and Church 1979). In particular, Nowell and Church, in an investigation representing flow over a gravel substratum, found that a log-velocity model was not valid closer to the bed than $Z/D = 0.35$ and that turbulence intensity changed character below $Z/D = 0.20$. In the present report the lowest velocity determination was at 2.5 cm above the bed, which is equal to $Z/D \sim 0.20$. Consequently, none of the velocity profile data need correlate with detailed siltation processes if Einstein's (1968) hypothesis is correct.

Further investigations of the detailed mechanics of siltation in gravel beds will require hydrodynamic data very close to the bed or within the void spaces of the surface gravels.

Deposition Rate

Deposition rates are largely independent of the mass flow hydraulic parameters but are controlled by the gross suspended sediment concentration and the exchange velocity across the "zero" velocity plane, which in this instance was situated one grain diameter below the surface.

A mean deposition rate of $1.34\%\cdot h^{-1}$ for low suspended sediment concentrations of fine sand is less than the rate ($5.7\%\cdot h^{-1}$) reported by Beschta and Jackson (1979) for coarse sand. Nevertheless, even at low concentrations siltation is rapid regardless of the gross hydraulic properties of the flow or of the grain size of sand.

The conclusion that gross flow hydraulic parameters are of little utility in deposition studies over gravel beds is contrary to the findings of Beschta and Jackson (1979) where, with concentrations 1 cm above the bed of the order of 12 000 $mg\cdot L^{-1}$, deposition increased with Froude number. Beschta and Jackson's concentrations correlated with Froude number so that it is difficult to isolate the effect of either factor on deposition rates. Their concentrations were higher than used in the present investigation and may have influenced the flow dynamics. The concentration at which particle interaction influences flow has not been determined precisely. Lumley (1978) suggested a volume concentration of 0.003, which is equivalent to an approximate mass concentration of quartz particles of 8000 $mg\cdot L^{-1}$. High suspended sediment concentrations, especially near the bed, may reduce vertical eddy diffusivity. This process would increase the likelihood of deposition. Such a modification has been used to explain enhanced deposition from flows containing high concentrations of fine particles (Mucher and de Ploey 1977). However, although it can be inferred from the shear stress data (Table 2) that turbulence intensity was damped by high concentrations in this investigation, there is no specific information on turbulence structure. Certainly there is no evidence in Fig. 5 of significant enhanced deposition at high concentrations.

Downstream Siltation Rate

No field data for siltation within gravels to support equation 7 are known to the author. If equation 7 is rewritten and expressed as the reduction in suspended sediment concentration as an exponential function of distance from the source, supporting data are available. For example, Shapley and Bishop (1965) and Miner (1968) reported a downstream reduction in concentration of total suspended solids from an experimental point release in a natural stream that would appear to fit a negative exponential function. Einstein (1968) found that the concentration of particles (3.5–30 μm in size) decreased exponentially downstream as sediment was deposited in an open-work gravel.

However, Krone (1962), who also found an exponential function for silty clay at low concentrations (< 300 mg·L^{-1}), observed a logarithmic function for high concentrations.

In uniform flow, one can expect the probability of deposition/resuspension to remain constant downstream (Einstein 1968), and yet p changed slightly in a downstream direction. Einstein observed that coarser grains were deposited upstream and fines were transported farther downstream. The grain size of the deposited sediment in the present experiments also decreased downstream, and yet incorporation of a reduced grain size with distance downstream did not suffice to correct the theoretical curve to fit the observed data (Fig. 6).

Solution of the equation $p = (1 - \tau_0/\tau_l)k$ for $p = 0.60$, $k = 1$, and for τ_0 (Table 2, column 9) yields a substantial value for τ_l in each instance. Values of τ_l should be equivalent to τ_c for fine sediment, and other factors, subsumed by k, should decrease or increase deposition rates (McCave and Swift 1976). Values of τ_c for the fine and coarse sands, obtained from threshold curves presented by Miller et al. (1977), are in the range 0.10–0.69 N·m^{-2}. Arguing from the ratio τ_0/τ_c alone would indicate that little deposition should have occurred (i.e. $p \simeq 0$). Camp (1943) argued that the deposition is a function both of V_s/U_*, which is analogous to $(1 - \tau_0/\tau_l)$ and to a turbulence parameter, $V_sD/2\epsilon$. When turbulence is great, the value of $V_sD/2\epsilon$ is low and the deposition rate is reduced. At low deposition rates ($V_s/U_* < 0.40$) the effect of turbulence in reducing deposition is negligible. Using Camp's method, for the low concentration data, derived theoretical values of p fall into two groups: $p > 0.70$, which represents transport largely by bedload, and $p < 0.35$, which are all suspended sediment runs. The calculated values of $p < 0.35$ contrast with the measured values of $p \simeq 0.60$. Clearly, turbulence should have a minimal effect. However, Camp was arguing only for deposition from suspension to a bed of similar loosely deposited material where resuspension could easily occur. In contrast, the experimental gravels were porous and could physically entrap particles in the dead zones in the lee of gravel grains and prevent resuspension.

Formation of a Surface Sand Seal

Beschta and Jackson observed that 0.55-mm sand formed a seal 5 cm thick at the surface of their 15-mm gravel as sand grains bridged openings to void spaces. In contrast, in the present experiments, 1.4-mm sand only formed a "patchy" seal over 15.57-mm gravel (p. 265). A partial explanation for the "patchy" nature of infiltration into a graded gravel bed is given below.

If equal-diameter spheres are packed systematically to form a bed there is a maximum diameter of smaller grains that may enter the interstices. The ratio of the two grain sizes is 0.154 if the spheres are tightly packed and 0.414 if loosely packed. Grains larger than the critical ratio can only be found in the void space if packed simultaneously with the large spheres (Fraser 1935, p. 919; Pettijohn 1975, p. 73). The ratio of the mean grain size of the silting sands and the gravel in both investigations falls in the range 0.010–0.090; consequently, one would expect infiltration in a bed consisting of uniform gravel. In mixtures of particles, porosity varies spatially no matter how carefully the proportions are mixed (Fraser 1935, p. 928–932) so that the degree of sand infiltration inevitably will be variable.

Practical Application for Fisheries

The experiments were designed to pertain to small shallow upland streams with well-graded gravels, and experiments are being conducted in the field to compare with the laboratory investigation. However, care must be taken in attempting to extrapolate the results to larger rivers with increased depths and poorly sorted gravels. A number of conclusions can be drawn, however.

Notably, even at low concentrations siltation is rapid regardless of the gross hydraulic properties of the flow or of the grain size of the sand. The gravel entrapped suspended material increasing the deposition rate to values in excess of those expected from simple settling theory. The implication is that where sediment pollution is frequent or continuous, gravel beds would require very frequent flushing. Without natural disturbance of gravels by high flows, mechanical cleansing would not appear to be advantageous unless the pollution incident is unlikely to reoccur.

Hydraulic parameters, velocity and depth in particular, act to control the downstream distribution of the sediment load rather than the overall magnitude of deposition. In straight reaches of small streams, without extensive pool and riffle development equation 7 may be appropriate to demonstrate the degree of siltation from a hypothetical point source and the length of stream affected.

Further laboratory research should concentrate on deposition in poorly graded gravel beds with detailed flow and suspended sediment data from very close to the bed. Field studies are required to verify the laboratory studies.

Acknowledgments

The project was funded by the Department of the Environment, the Natural Environment Research Council, the Northumbrian Water Authority, the Water Research Centre, Ministry of Agriculture, Fisheries and Food, and the Welsh Office. Professor G. Kelling made available the flume in the Department of Geology, University of Keele, and Professor P. Novak supplied a sediment hopper. Drs D. T. Crisp, D. J. J. Kinsman, and M. R. Leeder critically read the manuscript.

References

ADAMS, J. N., AND R. L. BESCHTA. 1980. Gravel bed composition in Oregon coastal streams. Can. J. Fish Aquat. Sci. 37: 1514–1521.

ANONYMOUS. 1981. Salmon-spawning gravel: a renewable resource in the Pacific North-west? Proc. Conf. Seattle, 6–7 Oct. 1980, The State of Washington Water Resources Centre, Pullman, WA. 285 p.

BAYAZIT, M. 1976. Turbulence characteristics in flow over large roughness elements. Disa Inf. 19: 26–29.

BESCHTA, R. L., AND W. L. JACKSON. 1979. The intrusion of fine sediments into a stable gravel bed. J. Fish. Res. Board Can. 36: 204–210.

CAMP, T. R. 1943. The effect of turbulence on retarded settling. Proc. 2nd Hydraul. Conf. Univ. Iowa Stud. Eng. Bull. 27: 307–317.

CARLING, P. A., AND N. A. READER. 1982. Structure, composition and bulk properties of upland stream gravels. Earth Surf. Process. Landforms 7: 349–365.

CHURCH, M., AND R. KELLERHALS. 1978. On the statistics of grain-size variation along a gravel river. Can. J. Earth Sci. 15: 1151–1160.

COLEMAN, N. L. 1981. Velocity profiles with suspended sediment. J. Hydraul. Res. 19: 211–229.

DEIGAARD, R. 1980. Longitudinal and transverse sorting of grain sizes in alluvial rivers. Inst. Hydrodyn. Hydraul. Eng. Tech. Univ. Denmark Ser. Pap. No. 26: 108 p.

DRAPER, N. R., AND H. SMITH. 1966. Applied regression analysis. Wiley, New York, NY. 407 p.

EINSTEIN, H. A. 1968. Deposition of suspended particles in a gravel bed. J. Hydraul. Div. Am. Soc. Civ. Eng. 94: 1197–1205.

FRASER, H. J. 1935. Experimental study of the porosity and permeability of clastic sediments. J. Geol. 43: 910–1010.

GRASS, A. J. 1971. Structural features of turbulent flow over smooth and rough boundaries. J. Fluid Mech. 50: 233–255.
HERBERT, D. W. M., J. S. ALABASTER, M. C. DART, AND R. LLOYD. 1961. The effect of china-clay waste on trout streams. Int. J. Air Water Pollut. 5: 56–74.
IWAMOTO, R. N., E. O. SALO, M. A. MADEJ, R. L. MCCOMAS, AND R. L. RULIFSON. 1978. Sediment and water quality: a review of the literature including a suggested approach for water quality criteria with summary of workshop and conclusions and recommendations. U.S. Environ. Prot. Agency 910/9-78-048: 151 p.
KRONE, R. B. 1962. Silt transport studies utilising radioisotopes. Final Rep. Inst. Eng. Res., University of California, Berkeley, CA.
LEE, D.-Y., W. LICK, AND S. W. KANG. 1981. The entrainment and deposition of fine-grained sediment in Lake Erie. J. Great Lakes Res. 7: 224–233.
LUMLEY, J. L. 1978. Two-phase and non-Newtonian flows, p. 289–324. *In* P. Bradshaw [ed.] Topics in applied physics. 12. Springer, New York, NY. 335 p.
MCCAVE, I. N. 1970. Deposition of fine-grained suspended sediment from tidal currents. J. Geophys. Res. 75: 4151–4159.
MCCAVE, I. N., AND S. A. SWIFT. 1976. A physical model for the rate of deposition of fine-grained sediments in the deep sea. Bull. Geol. Soc. Am. 87: 541–546.
MELAND, N., AND J. O. NORRMAN. 1969. Transport velocities of individual size fractions in heterogeneous bed load. Geogr. Am. Ser. A 51: 127–144.
MILLER, M. C., I. N. MCCAVE, AND P. D. KOMAR. 1977. Threshold of sediment motion under unidirectional currents. Sedimentology 24: 507–527.
MINER, N. H. 1968. Natural filtering of suspended soil by a stream at low flow. Pac. Northw. For. Range Exp. Stn. U.S. For. Serv. Res. Note PNW-88: 4 p.
MUCHER, H. J., AND J. DE PLOEY. 1977. Experimental and micromorphological investigation of erosion and redeposition of loess by water. Earth Surf. Process. 2: 117–124.
MULHEARN, P. J., AND J. J. FINNIGAN. 1978. Turbulent flow over a very rough random surface. Boundary-Layer Meteorol. 15: 109–132.
NEWSON, M. 1980. The erosion of drainage ditches and its effects on bedload yields in mid-Wales. Earth Surf. Process. 5: 275–290.
NOWELL, A. R. M. 1978. Dissipation of fine-scale structure in turbulent open-channel flow. Water Resour. Res. 14: 519–526.
NOWELL, A. R. M., AND M. CHURCH. 1979. Turbulent flow in a depth-limited boundary-layer. J. Geophys. Res. 84: 4816–4824.
NUTTALL, P. M. 1972. The effects of sand deposition upon the macroinvertebrate fauna of the River Camel, Cornwall. Freshw. Biol. 2: 181–186.
OWEN, M. W. 1969. Discussion of: Deposition of suspended particles in a gravel bed. J. Hydraul. Div. Am. Soc. Civ. Eng. 95: 1085–1087.
PETTIJOHN, E. J. 1975. Sedimentary rocks. 3rd ed. Harper International, New York, NY. 628 p.
RICHARDS, K. S. 1979. Channel adjustments to sediment pollution by the china-clay industry in Cornwall, England, p. 309–331 *In* D. D. Rhodes and G. P. Williams [ed.] Adjustments of the fluvial system. Kendall-Hunt, Dubuque, IA.
ROBINSON, M. 1980. The effect of pre-afforestation ditching upon the water and sediment yields of a small upland catchment. Inst. Hydrol. (U.K.) Rep. No. 73: 69 p.
SCHLICHTING, H. 1968. Boundary-layer theory. 6th ed. McGraw-Hill, New York, NY.
SHAPLEY, S. P., AND D. M. BISHOP. 1965. Sedimentation in a salmon stream. J. Fish. Res. Board Can. 22: 919–928.
SMITH, B. D. 1980. The effects of afforestation on the trout of a small stream in southern Scotland. Fish. Manage. 11: 39–58.
STOW, D. A. V., AND A. J. BOWEN. 1980. A physical model for the transport and sorting of fine-grained sediment by turbidity currents. Sedimentology 27: 31–46.
SUNDBORG, A. 1958. A method for estimating the sedimentation of suspended material. Ext. C. R. Rapp. Assoc. Gen. Toronto 1: 249–259.
TURNPENNY, A. W. H., AND R. WILLIAMS. 1980. The effects of sedimentation on the gravels of an industrial river system. J. Fish Biol. 17: 681–693.
WOLMAN, M. G., AND A. P. SCHICK. 1967. Effects of construction on fluvial sediment, urban and surburban areas of Maryland. Water Resour. Res. 3: 451–464.
ZAGNI, A. F. E., AND K. V. H. SMITH. 1976. Channel flow over permeable beds of graded spheres. J. Hydraul. Div. Am. Soc. Civ. Eng. 102: 207–222.

Appendix: Notation

C_0	Suspended sediment concentration at source	$mg \cdot L^{-1}$
D	Depth	m
d_{50}	Grain size at 50% percentile	m
F	Froude number	—
f	D'Arcy–Weisbach coefficient	—
g	Acceleration due to gravity	$m \cdot s^{-2}$
K_s	Bed roughness	m
k	Deposition coefficient	—
L	Distance from source	m
Q	Discharge	$m^3 \cdot s^{-1}$
R	Hydraulic radius, sediment feed rate	m, $g \cdot min^{-1}$
S_e	Energy slope	rad
U	Velocity	$m \cdot s^{-1}$
U_*	Shear velocity	$m \cdot s^{-1}$
V_s	Terminal settling velocity	$m \cdot s^{-1}$
Z	Height above bed	m
z	Coefficient for sediment turbulent transfer	—
z_0	Roughness length	m
γ	Specific weight of water	$kg \cdot m^{-3}$
ρ	Density of water	$kg \cdot m^{-3}$
ν	Kinematic viscosity	$cm^2 \cdot s^{-1}$
τ_0	Shear stress	$N \cdot m^{-2}$
Δ'	Raw deposition rate	$g \cdot m^{-2} \cdot h^{-1}$
Δ	Adjusted deposition rate	$\% \cdot h^{-1}$; $g \cdot m^{-2} \cdot h^{-1}$
p	Deposition coefficient	$m \cdot min^{-1}$
ϵ	Depth mean diffusion coefficient $= 0.0667\, D\bar{U}\sqrt{f/8}$	$cm^2 \cdot s^{-1}$
κ	von Kármán's constant	—

Subscripts

b = bed
c = critical
l = limiting
p = pots
s = sediment

Numerical subscript is height above bed in centimetres except for grain size data where values are percentiles.

Resource Management Biology for the Edible Kelp *Cymathere triplicata*

William G. Roland

Marine Resources Branch, Ministry of Environment, Province of British Columbia, c/o Parliament Buildings, Victoria, B.C. V8V 1X5

Roland, W. G. 1984. Resource management biology for the edible kelp *Cymathere triplicata*. Can. J. Fish. Aquat. Sci. 41: 271–277.

Sporophytes of *Cymathere triplicata* appeared only in spring and density declined thereafter; overwinter mortality was 100%. Standing crop estimates were highest during May–July. Plants were heaviest and generally had the longest and widest laminae in July and August. Thickness of laminae increased through December, the greatest increase being in the basal part of the lamina. Sori were initiated in August and approximately 90% of plants were fertile by September. Epibiota were most abundant during August–October. Moisture content decreased 2–3% from spring through winter. A plot subjected to almost total harvest in August had approximately 50% recovery of standing crop after 1 yr and full recovery after 2 yr, compared with a control area. A comparable recovery rate was seen for a similar September harvest. Sustained yields for a region of coastline should be maintained if no more than 50% of the standing crop is removed by intensive harvesting within plots, and if harvesting is not allowed prior to spore production. Best quality laminae in terms of length, thickness, weight per area, and moisture content occurred in August and September.

Les sporophytes de *Cymathere triplicata* sont apparus seulement au printemps et leur densité a baissé ensuite; la mortalité au cours de l'hiver a été de 100 %. Les estimations de la biomasse ont été les plus élevées de mai à juillet. Les plantes étaient les plus lourdes et avaient généralement les lames les plus longues et les plus larges en juillet et août. L'épaisseur des lames a augmenté jusqu'en décembre, la plus grande augmentation se produisant dans la partie basale de la lame. Les sores ont commencé à apparaître en août et environ 90 % des plantes étaient prêtes à produire des spores en septembre. Les épibiotes étaient très abondants d'août à octobre. La teneur en eau a diminué de 2 à 3 % du printemps jusqu'à l'hiver. Dans un secteur récolté presque totalement en août, il y a eu rétablissement d'environ 50 % de la population exploitable après 1 an et rétablissement complet après 2 ans, par rapport à un secteur témoin. Un taux de rétablissement comparable a été observé pour une récolte similaire en septembre. Des rendements soutenus pour une région de ligne de côte devraient être maintenus si pas plus de 50 % de la biomasse n'est enlevé par une récolte intensive à l'intérieur des secteurs et si l'exploitation n'est pas permise avant la production des spores. C'est en août et septembre que l'on a observé les lames de meilleure qualité en termes de longueur, d'épaisseur, de poids par unité de surface et de teneur en eau.

Received June 7, 1983
Accepted October 18, 1983

Reçu le 7 juin 1983
Accepté le 18 octobre 1983

Cymathere triplicata, a montotypic genus in the Northeast Pacific Ocean, occurs attached to rocks in the upper subtidal (Setchell and Gardner 1925) and lower intertidal. The recorded distribution is from Puget Sound to the Bering Sea (Setchell and Gardner 1925).

Interest in utilizing *C. triplicata* for production of edible kelp products has made it the subject of culture studies (Druehl 1980a, 1980b, 1981) and wild harvest. High-quality plants are required, as the laminae are typically used following minimal processing to dry and remove unusable portions.

A field investigation was launched to generate the biological information needed for management of the edible kelp *C. triplicata* in conjunction with issuance of a Provincial licence for its harvest from western Queen Charlotte Strait. Standing crops of large concentrations of the kelp (W. G. Roland, unpubl. data) in this area were assessed and observations were made on aspects of population biology and plant quality. Recovery of standing crop after harvest was studied. Presented here are the results of this research. Biological aspects of resource management of this kelp are discussed in terms of sustained yield and plant quality.

Materials and Methods

Study Sites

One control and two harvest plots were established off the north coast of Malcolm Island (Fig. 1). A 30 × 60 m site was demarcated in July 1980 by corner buoys about 100 m east of Malcolm Point. The western half was randomly designated the harvest plot (plot B) and the remainder as the control (plot A). A second harvest plot (plot C, dimensions 10 × 10 m) was similarly demarcated in September 1980 in the approximate center of a commercially harvested portion of a *Cymathere* bed about 500 m east of plot A.

Depth in plots A and B ranged from 0 to 2.8 m below zero tide level and was approximately 3 m in plot C. The substrate in all three areas was cobbles and small boulders embedded in coarse

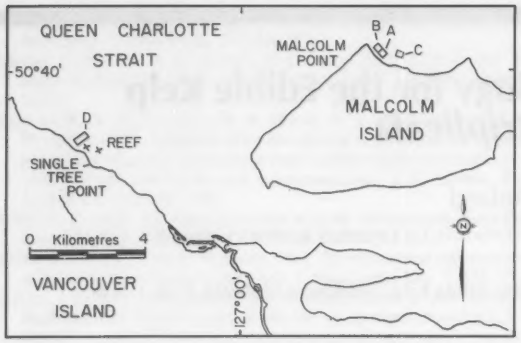


FIG. 1. Locations of study sites.

sand. A narrow, dense band of *Nereocystis luetkeana* occurred in the offshore half of plots A and B, and plot C was located in a *Nereocystis* bed. *Cymathere* and *Desmarestia viridis* provided most of the cover in the understory of plots A and B. No sea urchins were observed in plots A and B.

A 30 × 60 m study area (plot D) was demarcated off Single Tree Point in water ranging from 2.9 to 3.2 m below zero tide level. The substrate was composed of shell, cobbles, and small and occasional large boulders embedded in sand. Plot D was located just offshore of a dense *Nereocystis* bed, and this kelp was present in low density within the study area. The major contributors to cover within the plot were *Cymathere*, *Desmarestia ligulata* var. *ligulata*, *Alaria tenuifolia*, and *Laminaria groenlandica*. The red sea urchin *Strongylocentrotus franciscanus* and northern abalone *Haliotus kamtschatkana* occurred rarely on larger boulders.

Temperature, salinity, combined nitrite–nitrate nitrogen, and orthophosphate were monitored weekly during June–September and monthly otherwise at plots A and D 1 m above the seabed (Fig. 2). Sampling methods are given in Coon et al. (1982).

Solar radiation data (Fig. 2) were available from a pyranometer located at the Port Hardy Airport, approximately 10 km from plot D and 20 km from plot A (Environment Canada 1980, 1981).

Population Dynamics and Standing Crop

Sampling locations within the plots were randomly determined from tables of random numbers (Zar 1974). Scuba divers directed by a surface observer collected plants within a fixed radius quadrat for estimation of plant density and standing crop, and to provide a random sample of plants for morphological and plant quality measurements.

Since the plots were sampled six or seven times per year, a small quadrat size (0.25 m^2 at plot A and 0.5 m^2 at plot D) was chosen so that less than 1% of the study area would be sampled at any time. The small quadrat size, clumped distribution of plants, and inability to stratify sampling within the plot resulted in a fairly large variance for estimates of density and standing crop. Thirty quadrats per plot were collected each sample date to produce a standard error to mean ratio of approximately 0.3 for both variables. As density and standing crop estimates do not follow a normal distribution, the standard errors reported should be used with caution.

Young sporophytes were sampled at Malcolm Point in March 1981 by underwater counts; the plants were small and dense, thus making collection too time consuming. Biomass was estimated as the product of mean density and a mean weight per plant estimated from randomly collected plants.

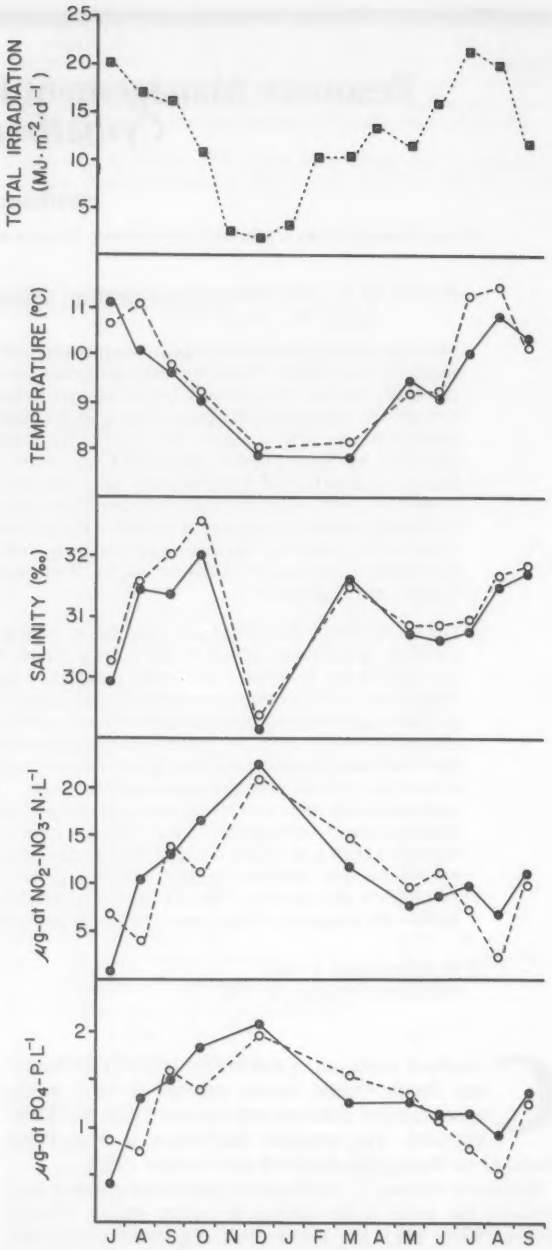


FIG. 2. Monthly mean temperatures, salinities, and nutrient levels from plots A (solid line) and D (broken line). Mean daily irradiation is for nearby Port Hardy Airport (Environment Canada 1980, 1981).

Macroflora Cover

Seasonal changes in the cover of understory macroflora in each plot (excluding canopy forming kelps, diatoms, and

encrusting algae) were monitored along a permanently placed 25-m-long lead line run diagonally over the seabed of each plot. The line was marked at 0.5-m intervals, and all macrophyte species overlying these points were recorded. Cover was calculated as a percentage of the total possible times that a taxon was observed. Repeat measurements of percent cover gave an average error of 10% for each taxon, and the percent error for each species was inversely related to its cover.

Harvesting

To evaluate recovery of an area after harvesting I chose control and harvest areas that (1) had a commercially harvestable quantity of *Cymathere* (greater than 50% cover), (2) were in close proximity, and (3) appeared similar in substrate, depth, and cover of other marine plants. The null hypothesis (H_o) that the standing crops in each were equal was tested with a Mann–Whitney *U*-test (Zar 1974) because data were not normally distributed and variances were unequal. After accepting the H_o the area was harvested; the same H_o was to be tested each subsequent year until the hypothesis was accepted and recovery concluded to be complete (unless rejected because the harvest plot contained more *Cymathere*). An α level of 0.20 was chosen. Increasing the probability of making a type I error provided more stringent requirements for choosing control and harvest areas and would tend towards conservatism when concluding that a harvest plot had recovered to control levels.

In August 1980, plot B was harvested by commercial divers. All detectable *Cymathere* plants with a lamina width greater than 10 cm (the minimum width arbitrarily permitted by the licence) were removed. Standing crop, density, lamina length and width, plant weight, and cover in plots A and B were sampled as previously described to establish the preharvest degree of similarity between harvest and control plots. Sampling was repeated in plot B immediately after harvest to determine the impact. Both plots were sampled in August 1981 and in June 1982.

Plot C was sampled in September 1980 both prior to and immediately following commercial harvesting. On both occasions ten 1-m^2 random samples were collected to estimate plant density and standing crop; cover was estimated along a 12.5-m-long lead line as previously described. Percent cover of macrophytes was estimated in May 1981 but from that date the area could not be relocated.

Measurements of Lamina Characteristics

On each sampling date the laminae of all plants collected from the plots were assessed for length, width, total weight, and presence of sori. Length was recorded as the greatest length; width was measured either at 30 cm above the lamina base or, if a lamina was shorter than 30 cm, at the point of greatest width. Thickness was measured with a micrometer caliper at the center and margin of laminae at points 5, 25, 60, and 100 cm from the lamina base. Lamina thickness, weight per unit area, and percent moisture were recorded for a random subsample of 30 plants.

Samples were stored in a large box for a maximum of 6 h and separated by moistened burlap sacks. Plants were soaked in seawater for several minutes prior to weighing. Fresh weight appeared to be maintained, since varied periods of soaking produced no change in weight. Weight per unit area of tissue from the lamina center and margin was determined from 6 × 2 cm samples cut at 20–30 cm from the lamina base. Plants were dried at 40–50°C until brittle and were then reweighed for estimation of percent moisture.

Epibiota

Epibiota were measured on at least 30 randomly sampled plants per plot on each sampling date. The area covered by the encrusting bryozoan *Membranipora* sp. and the number of primary stolons of the hydroid *Obelia* sp. were recorded for one randomly picked side of each lamina. The number of nesting gammarid amphipods was recorded for the entire lamina. Presence of green coatings of diatoms, which appeared when laminae were dried, were recorded for all plants used in estimation of dry weight.

Results

Population Dynamics, Standing Crop, and Cover of *C. Triplicata*

The birth rate of sporophytes at plot A was very low or nil after March sampling; less than 10% of plants sampled in May were less than 3 g wet weight and less than 3 cm wide. June or later samples never contained plants this small at either plot A or D. The mean plant size (Fig. 3) was much smaller in May 1981 at plot D, and many plants had juvenile characteristics, suggesting that the time of birth for most plants was later at that site. None of the previous year's plants were observed in March or May 1981, indicating that the plant is an annual in Queen Charlotte Strait as it is in Barkley Sound (Druehl 1980b).

The initial density of sporophytes was higher at plot A than at plot D; mortality was high during March–May 1981 at plot A, and thereafter was reduced (Fig. 4). Mortality rate at plot D was lower than at plot A after May 1981, and densities in both plots become more similar as summer progressed due to differing mortality rates. An apparent increase in density occurred at plot D in December 1980.

Standing crop increased dramatically in spring months with highest values occurring during May–July (Fig. 4). Standing crop can be considered a product of density and weight of sporophytes. Mean density decreased through spring and summer. Mean weight per sporophyte increased steadily from March to July. Thus, increased mean weight compensated for decreased density such that standing crop was maximal prior to or by July; thereafter, both declining density and plant weight resulted in reduced standing crops at both study sites. In 1981, standing crop peaked in May at plot A but peaked later at plot D, probably due to the rapid decline in density at plot A after May and small relative increase in plant weight after this date.

Total macroflora cover at plots A and D displayed a marked seasonality, with maximum cover in July and a minimum in December (Fig. 5). At plot A, *Cymathere* cover reached about 70% in July and August 1980 and then decreased to 28% in September and 2% in December. By the following March the cover of new sporophytes was 30%. This increased to 90% by May (coinciding with the standing crop maximum) and thereafter declined to 16% in September 1981. In June 1982 the cover was only 28%. The seasonal pattern of *Cymathere* cover at plot D was similar except that peak cover occurred after May 1981, as did standing crop.

An apparent increase in cover of perennial seaweeds occurred at both sites throughout the study. Cover of *L. groenlandica* was higher at plot D in 1981. Cover of *Laminaria yezoensis* and

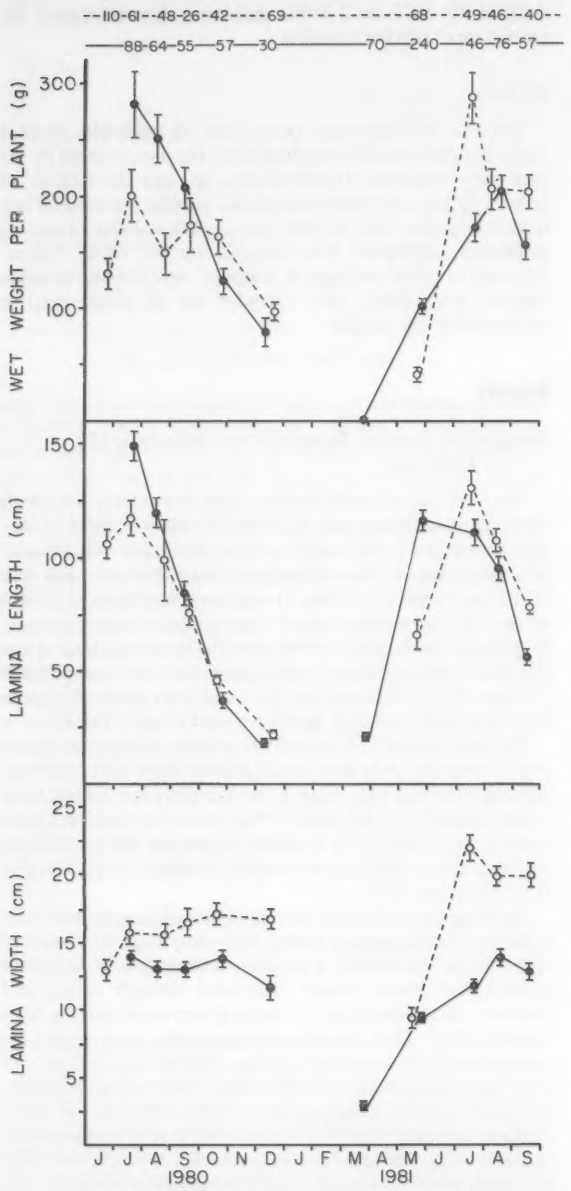


FIG. 3. Weight per plant, lamina length, and lamina width of *C. triplicata* at plots A (solid line) and D (broken line) ($\bar{x} \pm$ SE). Sample sizes corresponding to points are given at the top of the figure. Points are located to approximate the date of the sampling within each month.

Palmaria palmata at plot A increased steadily from 1980 through 1982.

Harvesting

At Malcolm Point, the control (plot A) and harvest (plot B) plots contained similar preharvest covers and standing crops ($\alpha = 0.20$) of *Cymathere* (Table 1). Harvesting reduced the mean standing crop, density, plant size, and cover of *Cymathere* (Table 1). By September 1980, the only notable change in cover

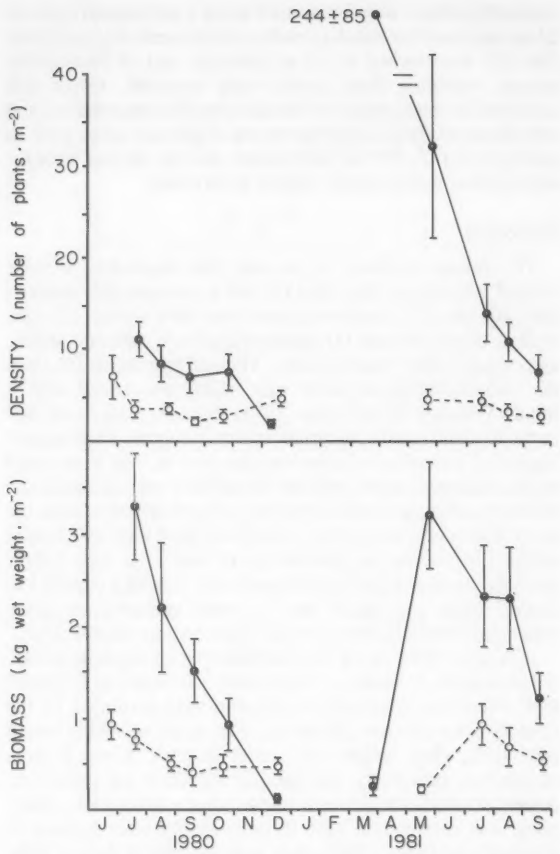


FIG. 4. Density and biomass of *C. triplicata* at plots A (solid line) and D (broken line) ($\bar{x} \pm$ SE). Points are located to approximate the date of sampling within each month.

of flora in the harvest plot was an increase in *P. palmata* from 4 to 14% (Fig. 5); in the control plot the cover of *Palmaria* decreased from 2 to 0%.

In August 1981, standing crop was significantly lower ($\alpha = 0.20$) at plot B and the cover of *Cymathere* was reduced. Cover of *Palmaria* had increased in both plots to 10–15% in the summer of 1981, and *L. yezoensis* had increased in both plots from approximately 2% cover in 1980 to 5–10% (control) and 10–15% (harvested). Changes in the cover of other flora were slight, and the total cover in the harvest plot was nearly always lower in 1981, indicating that the decrease in *Cymathere* was not accompanied by increases in other species. Density was also reduced by about 60% in the harvest plot in 1981; the decline in standing crop of only 50% is attributed to the presence of large plants in the harvest plot.

Standing crops of *Cymathere* in June 1982 were not significantly ($\alpha = 0.20$) different between plots A and B. Respective control and harvest plot covers were 27 and 31%. Both density and plant weight were higher in plot B (Table 1). Cover of *L. yezoensis* had increased to 19% in the control and 17% in the harvest plot; cover of other flora changed relatively little.

Plot C, in September 1980, had a preharvest *Cymathere* standing crop and cover of 2.9 $kg \cdot m^{-2}$ and 68%. This experiment did not have a good control; however, nearby plot A had

TABLE 1. Comparisons of standing crop, density, wet plant weight, and percent cover of *C. triplicata* between the control (A) and harvest (B) plots at Malcolm Point ($\bar{x} \pm$ SE, sample size in parentheses).

	A				B			
	Standing crop ($kg \cdot m^{-2}$)	Density ($No. \cdot m^{-2}$)	Plant weight ($g \cdot plant^{-1}$)	% cover	Standing crop ($kg \cdot m^{-2}$)	Density ($No. \cdot m^{-2}$)	Plant weight ($g \cdot plant^{-1}$)	% cover
Aug. 1980	2.2±0.7	8.5±2.0	250±22 (64)	72	2.2±0.6	11.2±3.1	197±15 (83)	60
Postharvest					0.3±0.1	0.8±0.3	151±29 (25)	4
Aug. 1981	2.3±0.6	10.8±2.1	204±15 (75)	43	1.1±0.4	4.6±1.5	287±29 (34)	23
June 1982	0.5±0.2	5.2±1.5	95±18 (39)	27	0.9±0.4	6.8±2.1	131±22 (51)	31

a standing crop of $1.5\,kg \cdot m^{-2}$ and 28% cover at this time. After harvest, the mean standing crop was reduced to less than $0.10\,kg \cdot m^{-2}$ and the cover to less than 4%. By May 1981 the cover of *Cymathere* was 64% compared with 90% in plot A; thus, a reduction due to harvest is suggested, since plot C had a greater crop and cover before harvest. Unfortunately, this area could not be relocated in September 1981 for a standing crop estimate to be made.

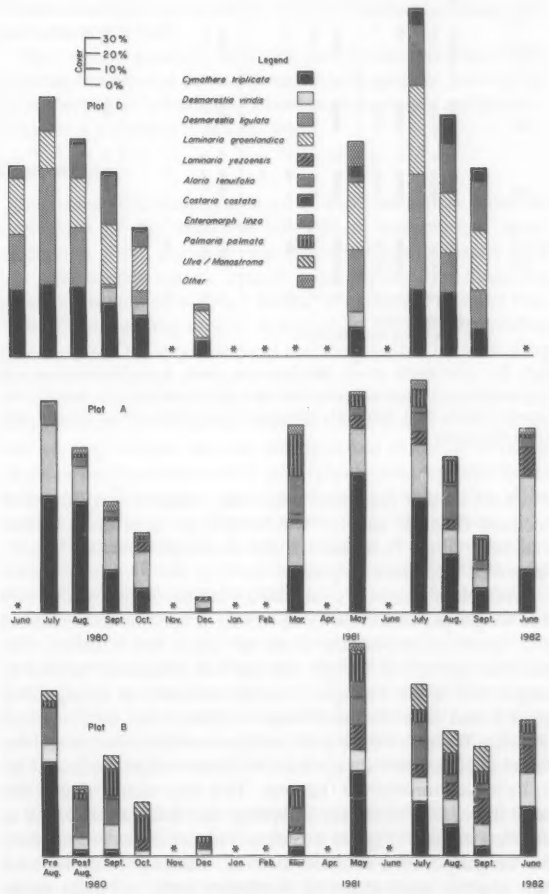


FIG. 5. Percent covers of macrophytes at plots A and D and harvest plot B. Asterisk indicates no sampling during that month. For plot B "pre" and "post" refer to the immediately pre- and post-harvest covers.

Presence of Sori

At plots A and D, sori were first observed in August (1980 and 1981), with approximately 20–30% of plants having soral tissue. Sori were located on the basal 20–30 cm of the laminae. Approximately 90% of plants were reproductive in September; this increased to nearly 100% in October and December.

In August, sori occurred mostly on larger plants (Table 2), and I used an analysis of variance to test the hypothesis that wet weight of plants with sori was greater than those without; years and sites were additional factors. The effect of sori presence or absence was highly significant ($P > 0.0001$) for both observed and ranked (Conover 1976) data. The test was performed on both data types because both the F_{max} test for homogeneity of variance and the Shapiro–Wilk statistics (SAS 1982) for normality showed deviations at $\alpha = 0.05$. The nonreproductive plants in September of both years were still among the smallest (generally less than 60 g wet weight), but by October, plants with a small wet weight also had sori (however, these could have been larger plants that developed sori and subsequently lost weight). Sori production was seasonal and early season reproduction occurred on larger plants.

Epibiota

Important epibiota were the encrusting bryozoan *Membranipora* sp. and nesting gammarids. These were most abundant during August–October (Table 3). Green patches of diatoms, which became apparent when laminae were dried, occurred on most plants by September and occurred more frequently on the distal (older and nongrowing) portions of laminae. The hydroid *Obelia* sp. occurred rarely.

Lamina Characteristics

Two general patterns of seasonal change in lamina characteristics were observed: (1) wet weight of plants and length and

TABLE 2. Wet weight (g) of *C. triplicata* plants ($\bar{x} \pm$ SD, sample size in parentheses) with and without sori collected during August 1980 and 1981 at plots A and D.

		Sori absent	Sori present
Plot A	1980	216±150 (49)	351±208 (16)
	1981	169±114 (62)	354±96 (14)
Plot D	1980	91±70 (33)	268±145 (15)
	1981	209±102 (23)	371±101 (11)

TABLE 3. Cover (cm^2) of the encrusting bryozoan *Membranipora* ($\bar{x} \pm$ SD) and percent occurrence of nesting gammarid amphipods on laminae of *C. triplicata* at plots A and D (sample size always greater than 30). Numbers of amphipods were recorded for each lamina sampled but rarely did more than one occur per lamina.

	Membranipora sp.		Nesting amphipods	
	A	D	A	D
1980				
July	44±102	4±5	0	0
August	448±238	12±34	20	4
September	160±370	28±64	21	28
October	146±358	64±236	1	45
December	0	0	0	0
1981				
March	0	0	0	0
May	0	0	0	0
July	2±4	Traces	6	0
August	32±64	Traces	16	4
September	120±140	10±16	7	18

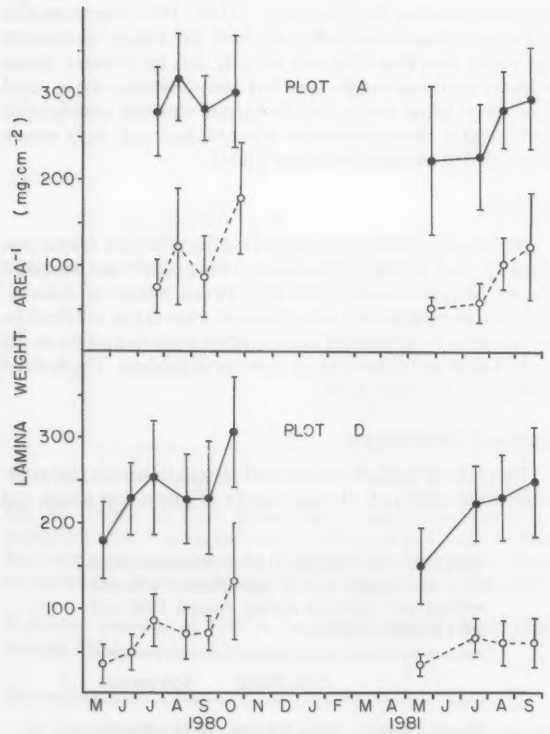


FIG. 6. Wet weight per area of lamina at plots A and D, sampled from the center (solid line) and margin (broken line), 20–30 cm from the laminae base ($\bar{x} \pm$ SD). Points are located to approximate the date of sampling within each month. Sample size was typically 30.

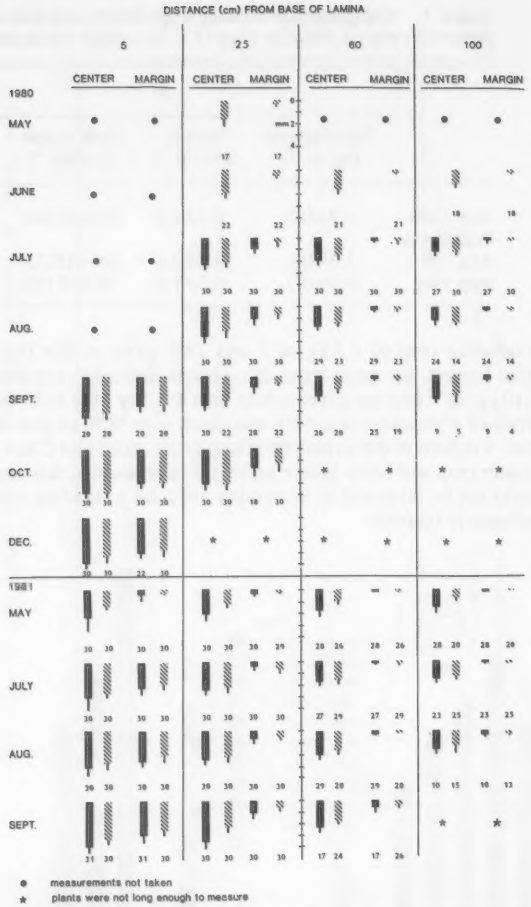


FIG. 7. Thickness of *C. triplicata* at plots A (solid bars) and D (hatched bars) (mean with one standard deviation is given; sample size appears below bar). Intervals between ticks on the central vertical axis are millimetres.

width of lamina increased until May–August and thereafter declined (Fig. 3) and (2) wet weight per area (Fig. 6) and thickness (Fig. 7) increased and moisture content (Fig. 8) decreased from birth of plants.

Fresh plant weight is a function of lamina length, width, and wet weight per area (this being mainly a function of thickness) plus a small contribution from the stipe and holdfast. The seasonal pattern of weight change was obviously related to length and width changes, which increased in spring from growth and later declined from erosion at the distal end of laminae. Weight–length relationships were not constant and the seasonal pattern not always parallel, since weight per area (Fig. 6) increased throughout the year. This was mainly due to the large increase in thickness. A spring–fall decrease of 2–3% in moisture content (Fig. 8) was observed, which would increase the weight per area of dried material. Lamina width declined only slightly after attaining maximum size, as blades erode relatively little at the margins.

Increases in thickness were primarily in the proximal region, as tissue 60 cm or more from the base changed little seasonally.

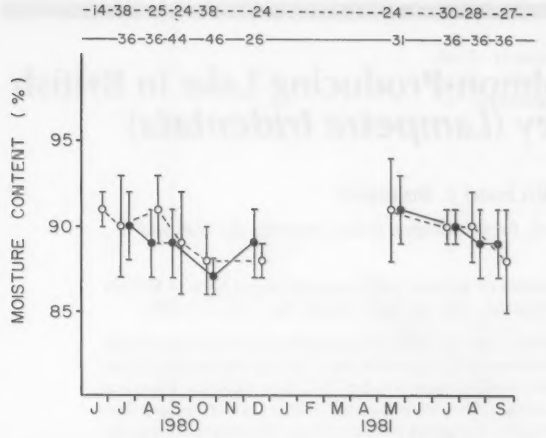


FIG. 8. Moisture content of *C. triplicata* at plots A (solid line) and D (broken line) ($\bar{x} \pm$ SD). Sample sizes corresponding to points are given at the top of the figure. Points are located to approximate the date of sampling within each month.

This basal increase in thickness correlated with the development and presence of sori.

Plant weight generally followed the seasonal pattern of light and temperature and inversely varied with nutrient levels (Fig. 2); however, the relationship between plant weight and productivity for *Cymathere* is not known.

Discussion

Sustained yield management of *C. triplicata* can be based on knowledge of the response of beds to harvest and spore production. First, standing crop recovered approximately 50% 1 yr after harvest and to control levels within 2 yr. Sustained yield for a region of coastline should be ensured if no more than 50% of the standing crop is removed by intensive harvesting within plots. One-year recovery may be possible by increasing the amount of spores available for settlement. Reducing the size of harvest plots to less than 30 × 30 m and leaving adjoining unharvested areas or further limiting catch within harvest areas may accomplish this. Second, sori appeared in August on larger plants and approximately 90% of all plants were reproductive in September. Harvesting done prior to September should be restricted so that more plants are left within harvest plots.

Large seasonality in standing crop and density renders estimation of monthly levels difficult. Any preharvest estimates of standing crop made to predict yield should be adjusted monthly to account for these changes. The large declines in density after March at plot A were similar to density changes in a bed of the annual kelp *N. luetkeana* studied by Foreman (1976). The increase in density at plot D in December 1980 may have resulted from immigration of plants into the study area from windward populations, as many sporophytes were attached to bivalve shells and were observed to be moved by slight water motion.

Large annual variation in standing crop also leads to uncertain prediction of yield from any previous estimates. Thus, industry may at times have difficulty estimating production or obtaining quotas due to reduced crop. Both the reduced density and standing crop in 1982 at plot A, coincident with increased cover of perennial seaweeds, and the comparatively lower density and standing crop and consistently higher cover of perennial seaweeds at plot D suggest reductions from interspecific competition. This implies that *C. triplicata* is a successional species or possibly dependent on removal of competing perennial seaweeds for continued persistence. This is analogous to Foreman's (1977) conclusion for the annual kelp *N. leutkeana*. Removing these competitors may increase yields of *C. triplicata*.

Important characteristics of edible kelp are a large thick lamina, low moisture content, lack of epibiota (Druehl 1980b), and possibly lack of sori. Harvesting at the peak of standing crop (May–July) may allow the harvester to collect the greatest biomass, but quality is of primary concern for this fishery. Longest and widest laminae occurred in July and August. These variables, however, may be a lesser concern to quality than thickness, as laminae are always thin (especially at the margins) 60 cm or more from the lamina base. The margins and center portions of laminae thicken considerably during August–October, yet the basal, center portions of laminae may be thick enough for use prior to July.

Druehl (1980b) concluded that not all optimal features of cultured *Cymathere* occur in any month and that August is probably the best time to harvest. Data presented here suggest this to be the case for wild stocks. However, the commercial operator found the increased thickness in September and October desirable and did not speak unfavorably of the presence of sori. Thin portions of the laminae and epibiota were considered undesirable and were removed during processing to improve product quality.

Acknowledgments

I wish to thank Michael Coon for providing me the opportunity to study this fishery. Ian Sutherland and Ronald Hall assisted me in all phases of this research. Michael Coon, Paul Breen, and John Richards provided valuable comments on the manuscript and Michele Depuit patiently typed the various drafts.

References

CONOVER, W. J. 1976. Practical nonparametric statistics. 2nd ed. John Wiley & Sons, Inc., New York, NY. 493 p.

COON, L. M., R. L. DEMARCO, AND W. G. ROLAND. 1982. Nearshore physical and chemical oceanographic data from Queen Charlotte Strait and Broughton Strait: 1979–1981. B.C. Mar. Resour. Branch Fish. Data Rep. No. 3: 77 p.

DRUEHL, L. D. 1980a. The development of an edible kelp culture technology for British Columbia. I. Preliminary studies. B.C. Mar. Resour. Branch Fish. Dev. Rep. No. 24: 46 p.

1980b. The development of an edible kelp culture technology for British Columbia. II. Second annual report. B.C. Mar. Resour. Branch Fish. Dev. Rep. No. 26: 43 p.

1981. The development of an edible kelp culture technology for British Columbia. III. Third annual report. B.C. Mar. Resour. Branch Fish. Dev. Rep. No. 32: 43 p.

ENVIRONMENT CANADA. 1980, 1981. Monthly radiation summary. Vols. 21 and 22.

FOREMAN, R. E. 1976. Ecology and population dynamics of *Nereocystis luetkeana*. Benthic Ecological Research Program. Report to British Columbia Marine Resources Branch. 89 p.

1977. Benthic community modification and recovery following intensive grazing by *Strongylocentrotus droebachiensis*. Helgol. Wiss. Meeresunters. 30: 468–484.

SAS. 1982. SAS user's guide: basics. SAS Institute Inc., Cary, NC. 923 p.

SETCHELL, W. A., AND N. L. GARDNER. 1925. The marine algae of the Pacific Coast of North America. Part III. Melanophyceae. Univ. Calif. Publ. Bot. 8: 383–898.

ZAR, J. H. 1974. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, NJ. 620 p.

Recent Colonization of a Major Salmon-Producing Lake in British Columbia by Pacific Lamprey (*Lampetra tridentata*)

Susan P. Farlinger and Richard J. Beamish

Department of Fisheries and Oceans, Resource Services Branch, Pacific Biological Station, Nanaimo, B.C. V9R 5K6

Farlinger, S. P., and R. J. Beamish. 1984. Recent colonization of a major salmon-producing lake in British Columbia by the Pacific lamprey (*Lampetra tridentata*). Can. J. Fish. Aquat. Sci. 41: 278–285.

Pacific lamprey (*Lampetra tridentata*) were first observed in Babine Lake, the largest natural lake wholly contained in British Columbia, in 1963 and are currently found along approximately 15% of the length of the lake near the outlet. The number of spawning adults in 1982 was estimated to be 7281. Since Babine Lake is a major nursery area for sockeye salmon (*Oncorhynchus nerka*), the colonization of this lake by a parasitic lamprey is of concern, particularly if the species can become nonanadromous. The colonization may be beneficial if a commercial fishery can be sustained and if the species does not begin to feed in freshwater. The reason for the recent colonization is unknown but it coincides with increased human manipulation of fishes and habitat, including the removal of a major rock slide, 65 km downstream of the lake.

La lamproie du Pacifique (*Lampetra tridentata*) a été observée pour la première fois dans le lac Babine, le plus grand lac compris entièrement dans les limites de la Colombie-Britannique, en 1963 et on la trouve actuellement sur environ 15 % de la longueur du lac, près de l'émissaire. En 1982, on estimait à 7281 le nombre d'adultes reproducteurs. Comme le lac Babine est une importante région d'alevinage du saumon nerka (*Oncorhynchus nerka*), la colonisation de ce lac par une lamproie parasite n'est pas sans causer d'inquiétudes, surtout si elle devenait non anadrome. Par ailleurs, si la lamproie pouvait être exploitée commercialement de façon soutenue et qu'elle ne commence pas à se nourrir en eau douce, la colonisation par cette espèce pourrait être avantageuse. On ignore la raison de cette récente colonisation, mais elle coïncide avec une manipulation accrue des poissons et de l'habitat par l'homme, dont l'enlèvement d'un important éboulis de roches à 65 km en aval du lac.

Received May 24, 1983
Accepted October 18, 1983

Reçu le 24 mai 1983
Accepté le 18 octobre 1983

The Skeena River in British Columbia is the second largest salmon-producing system on the west coast of Canada. The Babine River (Fig. 1) is the main tributary of the Skeena River and it flows out of Babine Lake, 402 km from the Pacific coast. Babine Lake is the largest natural lake that is wholly contained in the province of British Columbia. The lake is 150 km long, has a mean depth of 55 m, and a surface area of 491 km^2 (Johnson 1965). There is a recreational fishery in the lake; however, the lake is most important as the principal nursery area for sockeye salmon (*Oncorhynchus nerka*) of the Skeena River system.

In 1946, counts of live and dead salmon were first made in Babine Lake by Federal fisheries biologists for the entire sockeye salmon run. To make these counts, they established a fish counting fence across all of the river just downstream of the lake, and it is still in use. The first Pacific lamprey (*Lampetra tridentata*) was reported at the counting fence in 1963 (Jordan and Smith 1972); in 1971 a notation in the daily log produced at the counting fence stated that the number of lamprey had been "steadily increasing over the last few years."

The sockeye salmon spawning migration in Babine Lake from July to November traditionally provided salmon as food for local natives. Local native Indians whose families have fished sockeye salmon in the area for genertions were surprised when lamprey first appeared in the local streams. Our discussions with these Indians indicted that lamprey have had no place in their culture or remembered history. Other residents living beside small streams flowing into the lake reported that spawning lamprey were first observed in the late 1960s and early 1970s.

Pacific lamprey are known to be present in other tributaries of the Skeena River (Fig. 1). Fisheries personnel working in the Lakelse Lake and River as early as 1949 reported large numbers of lamprey (T. Bilton, Pacific Biological Station, Nanaimo, B.C., pers. comm.). Historically, lamprey have been present at Moricetown Canyon on the Bulkley River (Carl and Clemens 1948). A native of Moricetown relates tales of his father pickling lamprey 50 yr ago; another, an older woman, tells of other preparation methods. This incorporation of lamprey into local culture is not evident at Babine Lake.

Since there is no history of lamprey in this large and important lake, our study examined the extent of their colonization. With the development of methods for the identification of larval lamprey (ammocoetes) in British Columbia (Richards et al. 1982), we could determine if the species present in the streams were Pacific lamprey. In addition, we estimated the abundance of adults.

Materials and Methods

We conducted a general survey of lamprey distribution of streams and adjacent lakeshore using hand-held electrofishing equipment. All streams flowing into Babine Lake and Nilkitkwa Lake (Fig. 2) were surveyed from June to September 1981; in

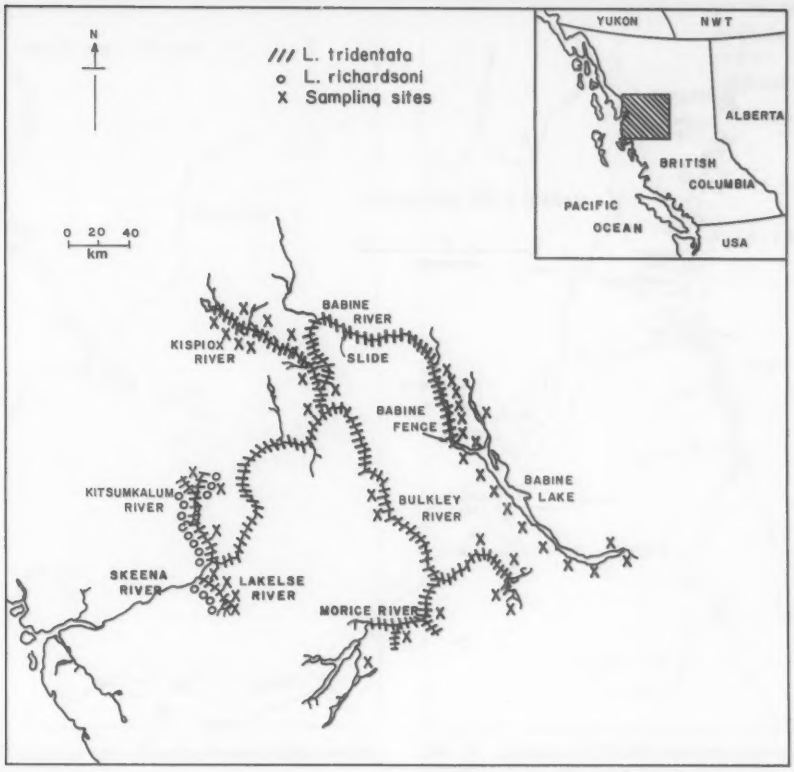


FIG. 1. Location of Skeena River and Babine Lake including the distribution of lamprey (*L. tridentata* and *L. richardsoni*) as determined in this study.

1982, streams at the edge of the distribution were reexamined. The presence of nests, spawning adults, or dead adults was also used to indicate the presence of lamprey. Lake shoreline adjacent to streams containing lamprey was surveyed from the surface and checked using scuba gear. In most locations, scuba observations did not reveal nests or adults that were not visible from the surface.

Minimum abundance of adults was estimated by counting nests during the spawning period. It was assumed that all nests contained eggs. Nests were 15–25 cm in diameter and 2–5 cm deep. They were easily identified by their silt-free appearance; however, not all nests were located in areas that could be surveyed. A factor was estimated to correct for the possibility that more than two lamprey used each nest and for nests that were not counted. The correction factor was determined by selecting one stream as an index. The number of lamprey in this stream each day of the spawning period was determined by summing the results of visual counts and numbers from traps set at the mouth of the stream. These counts were summed over the spawning period to produce the number of spawner days (Neilson and Geen 1981). Sex ratio was examined from samples of adults collected in the fall during their migration to the spawning areas and in the spring during spawning. Residence times were estimated for each sex by tagging (Floy anchor tag). The number of adults per nest was then estimated by dividing the spawner days for each sex by the resident times (Neilson and Geen 1981). Correction factors were then applied to the total counts of nests upstream of the Babine River counting fence.

Surveys of other streams and rivers in the Skeena system were undertaken to identify the distribution of Pacific lamprey. The area between sites that contained Pacific lamprey was considered to contain lamprey.

Adult lamprey were trapped at the mouth of Eel Creek using various sizes of conical or rectangular traps covered with 2.5-cm^2 mesh. Tunnels were inserted at both ends or at one end.

Samples of ammocoetes were obtained from streams, identified (Richards et al. 1982), and measured for total length.

Maturing adults migrating into Babine Lake from July to October were collected in traps at the counting fence and with dip nets from the river. Salmon fry traps set upstream of the counting fence in the spring captured ammocoetes.

Results

Distribution

Only ammocoetes of the Pacific lamprey were found in the Babine River and Lake system. Larval Pacific lamprey were found in all streams at the outlet end of Babine Lake, in Nilkitwa Lake, and in the connecting Babine River upstream of the counting fence (Fig. 2–5; Table 1). No lamprey were found between 9 Mile Creek and the inlet (Fig. 2; Table 1).

Ammocoetes were found in typical habitat of silt and detritus covered mud, in backwaters or near banks. In streams closer to the outlet (e.g. unnamed creeks 5 and 6, Fig. 4) ammocoetes were found as far as 1 km from the lake. In the streams farthest

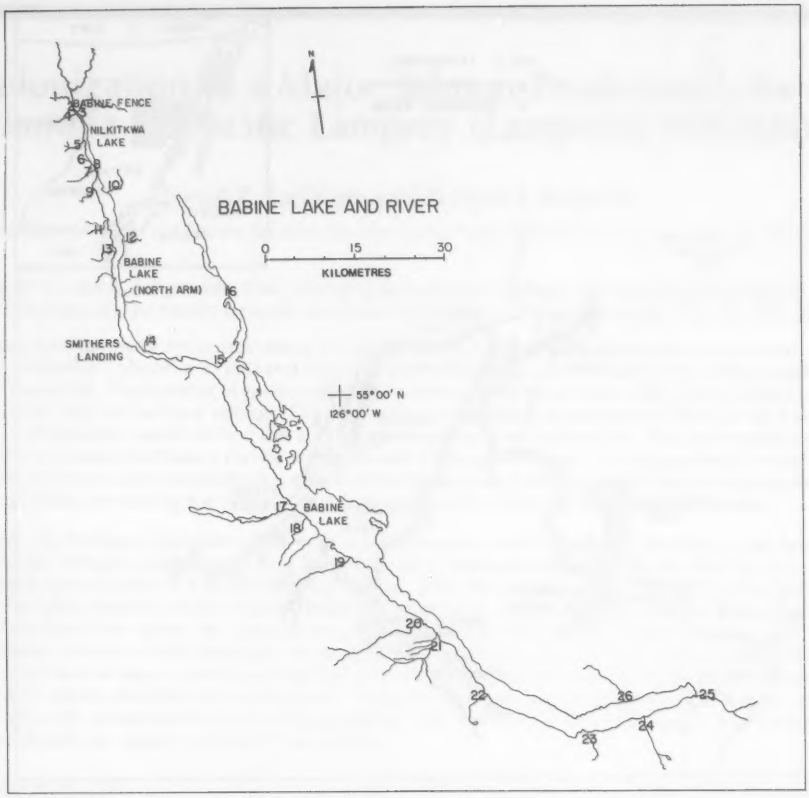


FIG. 2. Babine Lake and tributaries (see Table 1 for creek names).

from the outlet (e.g. Eel and 5 Mile Creek, Fig. 5) ammocoetes were found close to the mouth of the creek. In general, the larger ammocoetes were found closer to the mouth.

An intensive survey of Fulton River was made but no nests or ammocoetes were found. We have an unconfirmed report that from 1966 to 1968 small numbers of larval lamprey were captured in the fry traps in Fulton River (A. Coburn, Pacific Biological Station, Nanaimo, B.C., pers. comm.). The river was dammed in 1967 so it is possible that alterations to the river either prevented lamprey movement from the lake upstream of the dam or in some way changed the suitability of the river for lamprey spawning.

Ammocoetes ranged form 8 to 176 mm (Fig. 6). There are insufficient samples of *L. tridentata* ammocoetes from other rivers to permit quantitative comparisons of size; however, the data that are available (Kan 1975; Richards 1980; Pletcher 1963; R. J. Beamish, unpubl. data) suggest that ammocoetes from Babine Lake are larger than those found in many other river systems. (It is difficult to use larval length frequency data published prior to Richards 1980 because of the uncertainty of identification.) Metamorphosing lamprey collected in August and September of 1981 and 1982 ranged in size from 115 to 155 mm (Fig. 6), and these sizes also appear to be large for the species (Kan 1975; Beamish 1980; R. J. Beamish, unpubl. data; Richards 1980; Pletcher 1963).

Pacific lamprey ammocoetes were present in the Bulkley and Kispiox river systems (Fig. 1) and were found in the extreme headwater creeks of these systems. The Morice River is a well-known source of lamprey as evidenced by the name Lamprey Creek that flows into the Morice River. We did not find ammocoetes in the river flowing into Morice Lake, but the survey of this river was not extensive.

Adult Pacific lamprey are common in the upper Bulkley River and Bulkley Lake, Morice River, and the Kispiox River. Collections of ammocoetes and observations of adults indicate that Pacific lamprey ammocoetes were present in the Skeena River downstream of the Bulkley River. Our surveys of the Kitsumkalum and Lakelse rivers produced ammocoetes of *Lampetra richardsoni* as well as Pacific lamprey. The reports of adult lamprey in the Kispiox, Bulkley, and Morice rivers, the presence of ammocoetes in the extreme headwater creeks, and the incorporation of lamprey into local culture indicate that lamprey have had an historic presence in these rivers.

Spawning and Adult Biomass in Babine Lake

The occurrence of dead lamprey at the counting fence steadily increased after the first report of two dead lamprey washed against the counting fence on July 11, 1963 (F. P. Jordan, Pacific Biological Station, Nanaimo, B.C., pers. comm.). In our study, lamprey were observed migrating through the counting fence into Babine Lake from mid-July until mid-October. These migrants spawned from mid-June to late July in the following year (Beamish 1980) (Fig. 7, 8). Dead, spawned

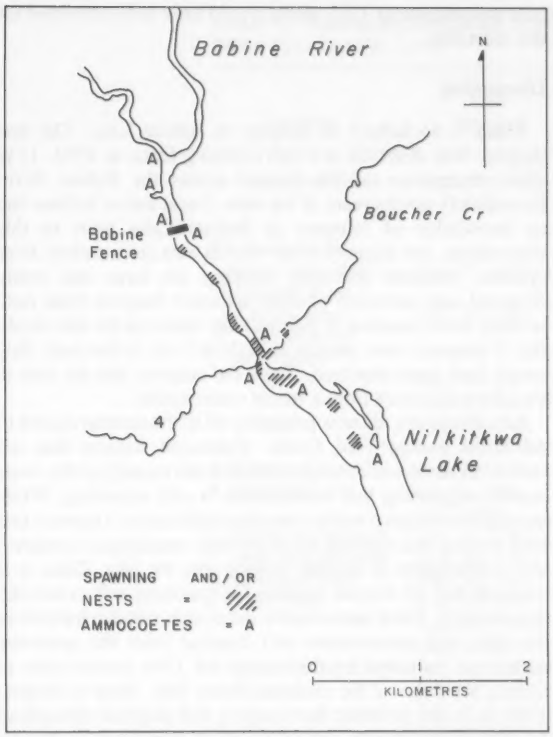


FIG. 3. Location of Pacific lamprey ammocoetes and adults immediately south of the counting fence.

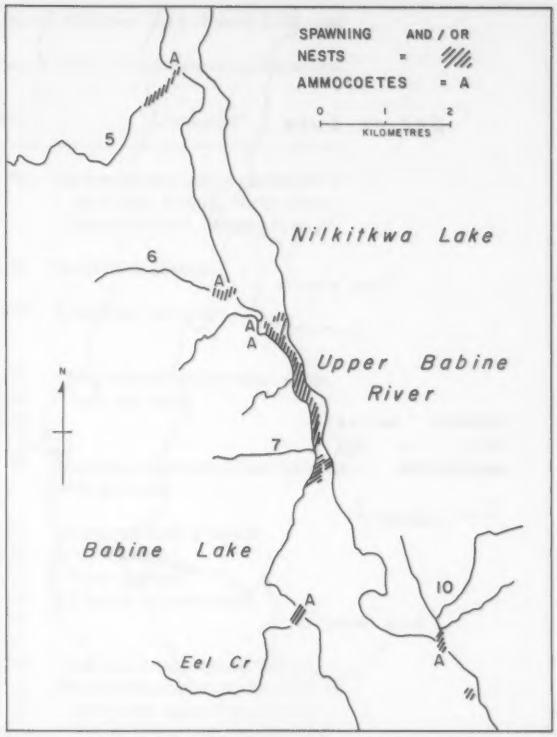


FIG. 4. Location of Pacific lamprey ammocoetes and adults in the Nilkitkwa Lake and upper Babine River area.

lamprey were washed downstream and some were retained at the counting fence.

Lamprey spawned from the counting fence to 9 Mile Creek (Fig. 2). Lamprey were observed to spawn in creeks as far as 1 km from the lake, although most nests were closer to the lake. In the upper Babine River, Nilkitkwa Lake, and lower Babine River, nests and spawners were observed in gravel shoals where there is a definite and consistent unidirectional flow at depths ranging from 30 cm in riffle areas to 4 m in cut bank areas. The deep (4 m) spawners were observed only in small numbers above Boucher Creek and at the Upper Babine River where it flows from the lake. The largest proportion of lamprey spawned in depths of 1 m or less.

Scuba dives were made in areas that were thought to be possible deep spawning areas. These included Babine Lake at unnamed creek No. 10, Babine Lake at Eel Creek, upper Babine River, and lower Nilkitkwa Lake. At the former two sites, there was a barely detectable movement of water over mud or hard sand bottom and no sign of lamprey spawning activity. In lower Nilkitkwa Lake at a consistent depth of 5 m, no sign of spawning was detected on the mud and weed bottom.

In Eel Creek, in both 1981 and 1982, the first spawners were observed on June 19. In 1982, over the next 10 d, the numbers in the creek rose rapidly to 143 spawners on July 1 (Fig. 8). After a freshet, numbers remained about 110 and then began to decline after July 9. (When high water levels prevented daily counts it was necessary to estimate daily abundance with the use of a predictive regression on the preceeding and following counts.) Spawning was complete by the end of July. Spawning occurred from the mouth of the creek to approximately 400 m up the creek.

A total of 141 mature lamprey were tagged at the mouth of the creek and 36 were recovered after spawning. The estimated residence time in the creek was 6.5 d for males and 4.6 d for females. The low recovery rate indicates that the estimated residence times may only approximate actual residence times. The sex ratio of 4 males to 3 females (Fig. 9) was determined from a sample of 252 fish, trapped at the entrance of Eel Creek as they moved into the creek during the spawning period. Samples of 357 adults collected during the upstream migration from mid-July to mid-September of 1979–82 had a sex ratio of 1:1. Because of the relatively small samples and because the fall migrants were not sampled continuously throughout their migration, it is not known if the change in sex ratio was real. Thus, the sex ratio of 4 males to 3 females was used in the population estimate. If the sex ratio of 4:3 results from increased mortality among females, possibly during the maturation process, then the estimate of number of lamprey at the time of fall migration will be larger.

The total number of spawner days was 3349, or 1914 male and 1435 female spawner days. Using the estimated residence times, the number of males was 294 (1914 ÷ 6.5) and females was 312 (1435 ÷ 4.6), or 606 lamprey. Since 120 nests were counted, the ratio of lamprey to nest counts was 0.462:1. This ratio was used to prorate the total nest count to estimate the total number of adults. The sex ratio determined from residence

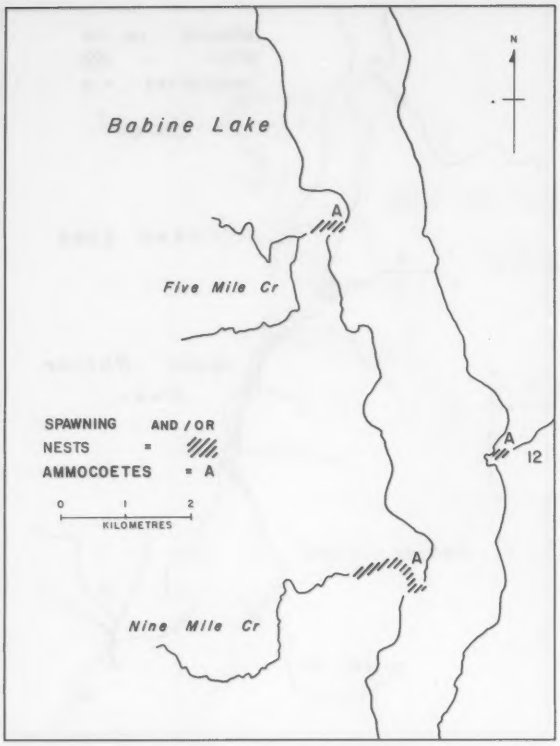


FIG. 5. Most southerly location of Pacific lamprey ammocoetes and adults in Babine Lake.

times is inconsistent with actual counts, suggesting that the factor used to prorate nest counts must be regarded as approximate.

Nest counts were made at the end of the spawning period (Table 2). The total number of nests counted upstream of the counting fence was 1442. Using a sex ratio of 4:3, the total number of adults was estimated as 7281. Because visibility was poor in some areas and in some creeks such as 5 Mile and 9 Mile Creeks, it is possible that the estimate is low even after correcting for unseen or destroyed nests or multiple use of nests. The amount of mortality that occurs from fall to spring is unknown. To estimate the number of lamprey moving into the lake the estimate of 7281 adults would have to be corrected for this mortality.

Discussion

There is no history of lamprey in Babine Lake. The first lamprey was observed at a fish counting fence in 1963, 17 yr after construction of this barrier across the Babine River immediately downstream of the lake. Local native Indians had no knowledge of lamprey in Babine Lake prior to this observation, yet lamprey were well known from nearby river systems. Because spawning lamprey are large and easily observed and carcasses of dead spawned lamprey have only recently been observed in Babine Lake there can be little doubt that if lamprey were present in Babine Lake in the past, they would have been observed. Thus, the lamprey that are now in the lake must result from a recent colonization.

Larval lamprey are now present in all of the streams closest to the outlet except Trail Creek. Colonized streams that are farthest from the outlet are populated in the vicinity of the creek mouth, suggesting that colonization is still occurring. While homing and straying studies were not undertaken, it appears that both homing and straying are occurring, resulting in a progressive colonization of streams flowing into the lake. Thus, it is probable that all streams suitable for spawning will eventually be colonized. Since ammocoetes do exist in suitable habitats in the lake, and ammocoetes will disperse from the spawning streams as indicated by the capture of 1344 ammocoetes in salmon fry traps at the counting fence from May to August 1982, it is also probable that lamprey will disperse throughout the lake. The ultimate size of the adult population in Babine Lake is difficult to determine; but the current population may be in an exponential growth phase, indicating that the final numbers should be considerably higher than the current estimate of 7281 adults.

Pacific lamprey are present and appear to be abundant in other tributaries of the Skeena River. At present there is no indication that they are a more important predator or competitor on commercial fishes in freshwater or salt water than the host of other predators and competitors. There is some evidence that recently metamorphosed Pacific lamprey will actively attack young salmon in salt water (Beamish 1980), and there is evidence that Pacific lamprey will attack adult sockeye salmon that are aggregating prior to return to freshwater (Williams and Gilhousen 1968; Beamish 1980). However, in salt water, Pacific lamprey feed on a variety of hosts (Beamish 1980) and

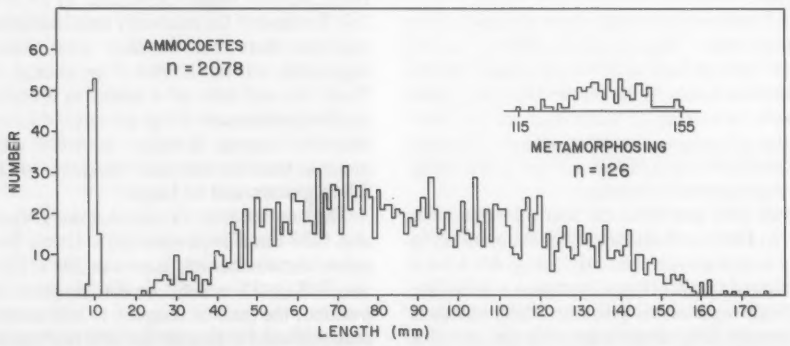


FIG. 6. Length frequency of Pacific lamprey ammocoetes collected in 1981 and recently metamorphosed juvenile adults collected in 1981 and 1982.

TABLE 1. Ammocoete distribution in tributaries of Nilkitkwa Lake, Babine Lake, and Babine River (see Fig. 2–5).

Location	Date surveyed	No.	Comments[a]
1, Nichyeskwa Creek	Aug. 17, 1981	78	On downstream side of confluence in mud bank. Nothing Nichyeskwa proper (100 m). No spawners
2A, Babine Lake below fence, west	Aug. 17, 1981	31	In silty side channel
2B, Babine River at fence, west	Aug. 17, 1981	148	In shallow backwater
2C, Babine River above fence			
East	Aug. 18, 1981	275	Along bank on shallow side. Other
	Aug. 22, 1981	320	side, not much
West	Aug. 25, 1981	49	
	Aug. 25, 1981	3	
3, Boucher Creek	Aug. 24, 1981	39	In marshy mouth area. Ammocoetes.
4, Unnamed creek	July 8, 1981		Only at mouth
	Aug. 1981		
5, Mouth of unnamed	Aug. 16, 1981	72	In large silt beds at mouth
creek 1 km upstream	Aug. 30, 1981	47	In silt by road
6, Unnamed creek	Aug. 30, 1981	72	0.5 km upstream
7, Trail Creek	Aug. 15, 1981	78	Silt banks at marsh outlet
	Aug. 21, 1981	78	
	Aug. 22, 1982	157	
8, Upper Babine River	Aug. 26, 1981	103	Upstream of Smokehouse Island
9, Eel creek	July 16, 1981	24	Most ammocoetes at mouth or farther
	July 17, 1981	20	out. Creek reduced to a trickle.
	July 28, 1981	121	Young-of-the-year found in mud
	Aug. 16, 1981	63	flats 30 m from mouth. A few larger, mostly young-of-the-year
10, Unnamed creek	July 17, 1981	45	Very large ammocoetes at mouth.
	Aug. 16, 1981	71	Nests found 100 m upstream
11, 5 Mile Creek	Aug. 9, 1981	9	Ammocoetes found only at mouth, shocked up 200 m. Nests seen up to 0.5 km.
12, Unnamed creek	Aug. 16, 1981	147	Only at mouth. Beyond 20 m, very little flow
13, 9 Mile Creek	July 16, 1981	8	Adult at mouth, nests to 1 km. Dead spawner 5 km
14, Unnamed creek	July 3, 1982		
	Oct. 11, 1982		
15, Unnamed creek	Oct. 11, 1982		
16, Morrison River	Aug. 9, 1981		
	July 3, 1982		
	Oct. 11, 1982		
17, Fulton River	July 13, 1981		
	Aug. 14, 1981		
	Oct. 14, 1982		
18, Tachek Creek	Aug. 13, 1981		
19, Sockeye Creek	Aug. 13, 1981		
20, Pierre Creek	Aug. 13, 1981		
21, Twain Creek			
22, Cross Creek			
23, Pinkut Creek			
24, 4 Mile Creek	Aug. 10–12, 1981		
25, Sutherland River			
26, 6 Mile Creek			

[a]No lamprey and no nests found at locations 14–26.

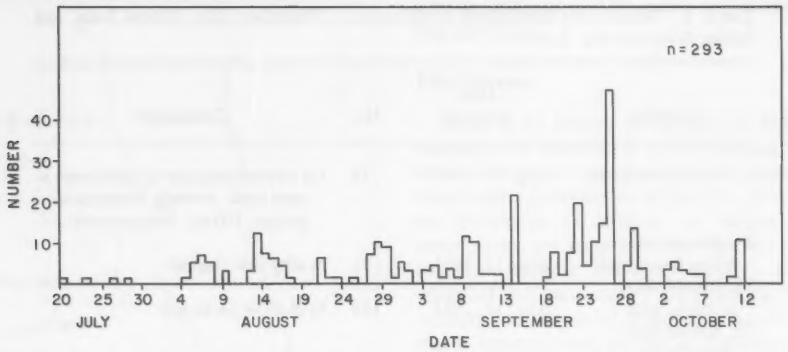


FIG. 7. Number of adult lamprey observed migrating through the counting fence during July–October 1982 (fence removed on October 12).

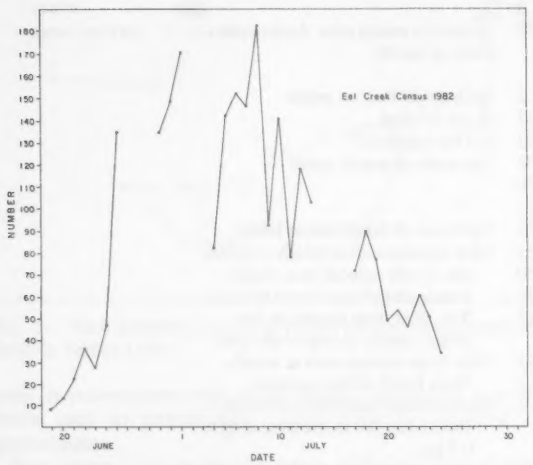


FIG. 8. Number of spawning lamprey observed in Eel Creek, 1982.

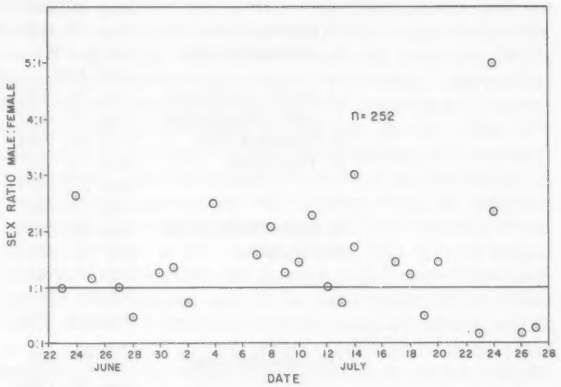


FIG. 9. Sex ratios of Pacific lamprey captured at the mouth of Eel Creek, 1982, during the spawning period.

TABLE 2. Nest counts in Babine Lake area in 1982 (see Fig. 2 for location of unnamed creeks).

Location	Date	Count
2C, Upstream of counting fence including mouth of Boucher Creek	July 28	557
4, Unnamed creek	July 23	25
5, Unnamed creek	July 20	46
6, Unnamed creek	July 20	4
8, Upper Babine River	July 26, 27	610
9, Eel Creek	July 24	120
10, Unnamed creek	July 5	25
11, 5 Mile Creek	July 26	50
13, 9 Mile Creek	July 26	5

there is no evidence of preference for important commercial species of salmonids.

There is evidence that Pacific lamprey prefer to feed on midwater species such as Pacific hake (*Merluccius productus*) and walleye pollock (*Theragra chalcogramma*) (Beamish 1980). Until more is known about Pacific lamprey in the ocean and the causes of mortality of salmon in the coean, there is no evidence to indicate that an increased lamprey production in the Skeena system will affect salmonids in salt water in the same manner as salmonids were affected in freshwater in the Great Lakes (Smith 1971).

A major impact on commercial species may occur if the Pacific lamprey can become landlocked (or nonanadromous) and if the abundance continues to increase in the lake. While it is postulated that the sea lamprey (*Petromyzon marinus*) can become nonanadromous, it is not known if the ability to adapt to a nonanadromous habit is a component of the genotype of the Pacific lamprey. There are no documented reports of Pacific lamprey feeding on freshwater fishes in any of the tributaries of the Skeena River, and the only documented example of important predation by lamprey on freshwater fishes in British Columbia is by *Lampetra macrostoma*, a species distinct from the Pacific lamprey (Beamish 1982). Thus, this question of whether or not the anadromous form can become nonanadromous is vital to the understanding of the consequences of the increased abundance in Babine Lake.

If it is found that the nonanadromous habit is part of the genotype of this species then the effect on resident fishes may be similar to the effect *L. macrostoma* has on resident fishes in Lake Cowichan and Mesachie Lake on Vancouver Island (Beamish 1982). In these lakes more than 50% of all salmonids have been observed to have lamprey scars. Younger fish are

attacked by lamprey, and 1- and 2-yr-old coho salmon (*Oncorhynchus kisutch*) have been killed or severely emaciated by lamprey attacks (Beamish 1982). The wounding and scarring data and the observed mortalities indicate that *L. macrostoma* is a major component of the causes of natural mortality for salmonids in these lakes. Because *L. macrostoma* spawns in the lake, it would be difficult to eliminate it from the lake. If the Pacific lamprey in Babine Lake becomes nonanadromous and behaves as *L. macrostoma* has, it will be a very important predator of salmonids in the lake.

There may also be benefits from an increased abundance of lamprey. Lamprey are an important commercial species in many countries (S. P. Farlinger and R. J. Beamish, unpubl. data). The lamprey in the Skeena River area are large and suitable for export. Because lamprey are esteemed as a food item, it is possible that a commercial fishery could develop if the sustained yield is sufficiently high.

It is useful to consider how the colonization into Babine Lake occurred. As shown, Pacific lamprey have been found in extreme headwaters of other tributaries of the Skeena River. According to local residents they have always been present and apparently abundant in the Kispiox River (Fig. 7), yet they have not migrated up the Babine River, beyond the Kispiox River into Babine Lake. It is possible that the population in the Skeena River is increasing and that movement into Babine Lake is a result of a normal expansion of the population. However, the Kispiox and Bulkley rivers (Fig. 7) both appear to be completely colonized, and as was observed in Babine Lake, it would be expected that colonization would continue in upstream areas before downstream rivers and streams are completely colonized. The lack of lamprey in the Babine River indicates that it was more than a naturally expanding population that provided the stimulus for lamprey to stray a little farther up the Babine River.

There have been several man-induced changes in the Babine Lake area. The counting fence was established in 1946 and the construction of several sockeye salmon enhancement facilities was initiated in the mid-1960s. These enhancement facilities were constructed after the initial observation of lamprey at the counting fence, indicating that colonization of the lake had already occurred. Thus, there does not appear to be a direct relationship between the colonization of Babine Lake and the establishment of enhancement facilities. It is unknown if the construction of the counting fence influenced the colonization.

In 1951 there was a major rockslide just upstream of the Kispiox River (Godfrey et al. 1954). The rockslide greatly restricted access of salmon to the lake in 1951 and 1952 and caused the loss of many thousands of fish and reduced spawning success. The rockslide occurred in an area of the river that was characterized by extremely swift water. The rockslide was removed in 1953 and the alterations to the river may have enabled lamprey to continue migrating up the river or in some way provided a stimulus to continue migration. Larval lamprey might have been introduced as bait into Babine Lake as a result of increased sports fishing activities in the late 1950s; however, there is little evidence to support deliberate or accidental introductions of lamprey.

Whereas the cause of colonization of Babine Lake is unknown there is little doubt that it has occurred recently. The effect of this colonization remains to be determined. The expected increase in abundance can be beneficial if a commercial fishery for lamprey develops but it may be extremely harmful if Pacific lamprey can and do become nonanadromous.

Acknowledgments

The field assistance of Mr G. A. Thomas and his helpful suggestions throughout the project were greatly appreciated. D. Southgate and staff at the counting fence provided equipment and accommodation. Fishery Officers Don Meyers, Terry Turnbull, Peter Waloshyn, and G. Cockell provided valuable assistance and information. Heidi Fargo, Ray Scarsbrook, and Mike Smith assisted in the collection of samples. Many other people provided assistance and information and we thank them for their advice and support.

References

BEAMISH, R. J. 1980. Adult biology of the river lamprey (*Lampetra ayresi*) and the Pacific lamprey (*Lampetra tridentata*) from the Pacific coast of Canada. Can. J. Fish. Aquat. Sci. 37: 1906–1923.

1982. *Lampetra macrostoma*, a new species of freshwater parasitic lamprey from the west coast of Canada. Can. J. Fish. Aquat. Sci. 39: 736–747.

CARL, G. C., AND W. A. CLEMENS. 1948. The freshwater fishes of British Columbia. B.C. Prov. Mus. Handb. No. 5. 1st ed.

GODFREY, H., W. R. HOURSTON, J. W. STOKES, AND F. C. WITHLER. 1954. Effects of a rock slide on Babine River salmon. Fish. Res. Board Can. Bull. 101: 100 p.

JOHNSON, W. E. 1965. The morphometry of Babine Lake and Nilkitkwa Lake. Fish. Res. Board Can. Manuscr. Rep. 819: 16 p.

JORDAN, F. P., AND H. D. SMITH. 1972. Summary of salmon counts and observations from the Babine River counting fence 1967–1979. Fish. Res. Board Can. Tech. Rep. 331: 63 p.

KAN, T. T. 1975. Systematics, variation, distribution and biology of lampreys of the genus *Lampetra* in Oregon. Ph.D. thesis, Oregon State University, Corvallis, OR. 194 p.

NEILSON, J. D., AND G. H. GEEN. 1981. Enumeration of spawning salmon from spawner residence time and aerial counts. Trans. Am. Fish. Soc. 110: 554–556.

PLETCHER, F. T. 1963. The life history and distribution of lampreys in the Salmon and certain other rivers in British Columbia, Canada. M.Sc. thesis, University of British Columbia, Vancouver, B.C. 195 p.

RICHARDS, J. E. 1980. Freshwater life history of the anadromous Pacific lamprey *Lampetra tridentata*. M.Sc. thesis, University of Guelph, Guelph, Ont. 99 p.

RICHARDS, J. E., R. J. BEAMISH, AND F. W. H. BEAMISH. 1982. Descriptions and keys for ammocoetes of lampreys from British Columbia, Canada. Can. J. Fish. Aquat. Sci. 39: 1484–1495.

SMITH, B. R. 1971. Sea lampreys in the Great Lakes of North America, p. 207–247. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 1. Academic Press, London and New York.

WILLIAMS, I. V., AND P. GILHOUSEN. 1968. Lamprey parasitism on Fraser River sockeye and pink salmon during 1967. Int. Pac. Salmon Fish. Comm. Prog. Rep. 18: 22 p.

Distributions of Ferrous Iron and Sulfide in an Anoxic Hypolimnion[1]

Robert B. Cook[2]

Lamont-Doherty Geological Observatory of Columbia University, Palisades, NY 10964
and
Department of Geological Sciences, Columbia University, New York, NY 10027

Cook, R. B. 1984. Distributions of ferrous iron and sulfide in an anoxic hypolimnion. Can. J. Fish. Aquat. Sci. 41: 286–293.

In the anoxic hypolimnion of Lake 227, Experimental Lakes Area, northwestern Ontario, ΣH_2S exhibits a mid-depth maximum, while Fe^{2+} increases with depth. At the mid-depth ΣH_2S maximum and below, saturation with respect to amorphous FeS is reached, and the concentration of ΣH_2S is limited by the high Fe^{2+} concentrations, in accord with the FeS solubility product. Values for pK_{sp} ($= a_{Fe^{2+}} \cdot a_{HS^-}/a_{H^+}$) for FeS determined from the ΣH_2S maximum and below averaged 3.16 in 1979 and agree well with other in situ and laboratory measurements. In the top 10 cm of sediment, pore water ΣH_2S and Fe^{2+} are in equilibrium with amorphous FeS. Analyses of cores confirms the existence of an iron sulfide phase. Fe^{2+}, which is produced in the pore water from the decomposition of organic matter, increases to concentrations at which siderite may form, although the presence of siderite has not been verified. Comparison of calculated pore water fluxes of Fe^{2+} with the observed increase of Fe^{2+} in the anoxic hypolimnion reveals that about 90% of the observed flux originates at the sediment–water interface, while the remainder is derived from pore water flux.

Dans l'hypolimnion anoxique du lac 227 de la région des lacs expérimentaux du nord-ouest de l'Ontario, ΣH_2S montre un maximum à mi-profondeur, tandis que Fe^{2+} augmente en fonction de la profondeur. Au maximum de ΣH_2S à mi-profondeur et plus bas, il y a saturation quant à FeS amorphe et la concentration de ΣH_2S est limitée par les fortes concentrations de Fe^{2+}, conformément au produit de solubilité de FeS. Les valeurs de pK_{sp} ($= a_{Fe^{2+}} \cdot a_{HS^-}/a_{H^+}$) pour FeS déterminées à la profondeur de ΣH_2S et plus bas en 1979 étaient en moyenne de 3,16, ce qui s'accordent avec d'autres mesures prises in situ et au laboratoire. Dans les 10 cm supérieurs de sédiment, ΣH_2S et Fe^{2+} de l'eau interstitielle sont en équilibre avec FeS amorphe. Les analyses de carottes confirment la présence d'une phase sulfure de fer. Fe^{2+} produit dans l'eau interstitielle à partir de la décomposition de matière organique augmente et atteint des concentrations auxquelles il peut se former de la sidérite, bien que la présence de cette dernière n'ait pas été vérifiée. Quand on compare les flux de Fe^{2+} calculés de l'eau interstitielle avec l'augmentation observée de Fe^{2+} dans l'hypolimnion anoxique, on constate qu'environ 90 % du flux observé prend naissance à l'interface sédiment–eau, tandis que le reste est dérivé du flux de l'eau interstitielle.

Received June 15, 1983
Accepted October 19, 1983

Reçu le 15 juin 1983
Accepté le 19 octobre 1983

The concentrations of solutes in interstitial waters of marine and lacustrine sediments provide a means of evaluating early diagenesis. Because of the large ratio of sediment to interstitial water in sediments, solute concentrations vary dramatically in response to diagenesis and are sensitive indicators of this process. In small lakes, the high ratio of sediment surface area to water volume in hypolimnia similarly promotes large variations in water column concentrations that can also be used to elucidate early diagenesis.

An early diagenetic process that occurs in interstitial waters is the microbially mediated conversion of iron (III) hydroxide and sulfate to Fe^{2+} and sulfide. These redox conversions, which are also coupled to nutrient and trace metal releases, may lead to iron sulfide formation. Equilibrium calculations in both marine and lacustrine sediments are often used to predict whether saturation with iron sulfide controls the concentration of Fe^{2+} or ΣH_2S (Spencer and Brewer 1971: Presley et al. 1972; Duchart et al. 1973; Emerson 1976; Elderfield et al. 1981; Giblin and Howarth 1983). There have been few studies in which equilibrium calculations were used in conjunction with measured sediment iron sulfide concentrations to verify diagenetic changes (Doyle 1968; Howarth 1979). Recently, Davison and Heaney (1978) examined Fe^{2+} and ΣH_2S interactions in the water column of an anoxic hypolimnion using measurements of Fe^{2+}, ΣH_2S, pH, and particulate FeS in the water column.

The objective of this study was to investigate the equilibrium processes controlling the Fe^{2+} and ΣH_2S concentrations in the water column and pore water of an anoxic hypolimnion. Measurements of the solid-phase chemistry of the sediments were also made to determine if the species predicted to have formed on the basis of the equilibria were actually present.

[1]Lamont-Doherty Geological Observatory Contribution No. 3535.
[2]Present address: Lake Superior Basin Studies Center, University of Minnesota at Duluth, Duluth, MN 55812.

Materials and Methods

Study Site

Lake 227 (L227) of the Experimental Lakes Area (ELA), near Kenora, Ont., was examined. The ELA was established in 1968 to study experimentally the chemical and biological processes that control eutrophication (Johnson and Vallentyne 1971). To this end, L227 received experimental, whole-lake additions of 0.55 g $P \cdot m^{-2} \cdot yr^{-1}$ from 1969 to the present (Schindler et al. 1973; Schindler 1975). Nitrate additions of 7.65 g $N \cdot m^{-2} \cdot yr^{-1}$ were made from 1969 to 1974 and 2.55 g $N \cdot m^{-2} \cdot yr^{-1}$ from 1975 to the present. Chlorophyll, an indicator of primary production, has increased 15–25 times as a result of the nutrient additions (Fee 1979).

L227 has a surface area of 5.0 ha, a maximum depth of 10.0 m, and a mean depth of 4.4 m (Brunskill and Schindler 1971). The hypolimnion exhibited seasonal oxygen depletion with anoxia below 9 m before the nutrient additions (Schindler 1971). After the nutrient additions, oxygen concentrations were below the detection limit deeper than 4 m for 10–11 $mo \cdot yr^{-1}$ (D. W. Schindler, Freshwater Institute, Winnipeg, Man., unpubl. data).

Sampling

In 1979, water samples were collected with a peristaltic pump at 4, 5, 6, 7, 8, 9, and 10 m at a station over the deepest point in the lake. Water for sulfide samples was pumped into glass syringes stoppered with sealed hypodermic needles. Iron samples were collected in standard BOD bottles by placing the pump outflow hose in the bottom of the bottle and allowing the bottle to overflow 2–3 times its volume prior to taking the sample. Samples for pH were pumped into polypropylene syringes.

Sediment pore water samples were taken with the close-interval dialysis membrane equilibrator (Hesslein 1976a, 1976b). The sampler consists of a series of 60 compartments milled into a sheet of Plexiglas at 1-cm intervals. Approximately 4 mL of distilled water was poured into each compartment, and membrane (0.2-μm pore size polycarbonate membrane) was placed over the compartments. To remove oxygen from the compartments, the apparatus was placed in a water-filled container through which nitrogen gas bubbled for approximately 10 h prior to use. Insertion into the sediments was done by slowly lowering the sampler into the soft sediment by cable from a boat. A platform, consisting of a Plexiglas frame and nylon screening material, attached to the sampler, halted penetration at 10 cm from the top of the sampler. The sampler was pulled out of the sediments after equilibrating with the pore water for a minimum of 10 d. Water for ΣH_2S, Fe^{2+}, and pH analyses was withdrawn from the sampler in the field using syringes equipped with hypodermic needles. ΣH_2S samples were immediately injected into sealed serum vials that contained a zinc acetate and NaOH solution for preserving the samples until analysis. Fe^{2+} samples were immediately injected into a 0.3 $mol \cdot L^{-1}$ HCl solution, and pH samples were kept in gas-tight syringes to prevent CO_2 loss.

Sediment samples were taken with a Wildco gravity corer fitted with a 5 cm (i.d.) acrylic core liner and sectioned within 1 h of collection. Subsamples for FeS, or acid-volatile sulfide (AVS) (Berner 1967), analysis were taken from each section, weighed, and then frozen. Another subsample was weighed, dried overnight at 60°C, reweighed to determine water content, and then analyzed for total iron.

Analytical Methods

Total H_2S was measured using the Lauth's violet method as modified by Stainton et al. (1977); the detection limit was 0.4 $\mu mol \cdot L^{-1}$ and precision was ±0.5 $\mu mol \cdot L^{-1}$. Ferrous iron was measured on acidified, unfiltered samples using 1,10-phenanthroline in the presence of an acetate buffer; the detection limit was 4.5 $\mu mol \cdot L^{-1}$ and precision was ±5 $\mu mol \cdot L^{-1}$. pH was measured potentiometrically, using a glass electrode standardized with NBS buffers. Sediment AVS was determined using the sulfide evolution method of Black (1965) with a 0.17 $mol \cdot L^{-1}$ NaOH solution as the trapping agent; the Lauth's violet technique was used for measuring the evolved sulfide. AVS analysis is a measure of the amorphous FeS, mackinawite (FeS), and greigite (Fe_3S_4) in a sample. Total iron in the sediments was measured on an aliquot of finely powdered sample using a Siemens SRF-1 X-ray fluorescence spectrometer.

Calculation of FeS Solubility

The reaction of concern is

(1) $H^+ + FeS \rightleftarrows Fe^{2+} + HS^-$

and the ion activity product (IAP) is given by

$$IAP = \frac{a_{Fe^{2+}} \cdot a_{HS^-}}{a_{H^+}}$$

where the amounts (moles per litre) of the various species are expressed as activities. Ionic strengths were calculated at each depth from Na^+, Mg^{2+}, Ca^{2+}, Fe^{2+}, HCO_3^-, NH_4^+, SO_4^{2-}, and Cl^- profile data (D. W. Schindler, Freshwater Institute, Winnipeg, Man., unpubl. results) and ranged from 0.8 to 1.5 $mmol \cdot L^{-1}$. The Debye–Huckel equation (Stumm and Morgan 1981) was used to calculate single ion activity coefficients for Fe^{2+} (range 0.85–0.90) and HS^- (range 0.95–0.97). HS^- concentration was calculated from ΣH_2S, pH, and the first dissociation constant for H_2S, which is $10^{-7.25}$ at 5°C (Smith and Martell 1976). The above formulation for FeS solubility avoids using the second dissociation constant for H_2S, the reported values for which span four orders of magnitude (Ellis and Giggenbach 1971; Giggenbach 1971; Davison 1980).

Results and Discussion

Water Column

Fe^{2+} increased with depth to a maximum of 650 $\mu mol \cdot L^{-1}$ in winter and 200 $\mu mol \cdot L^{-1}$ in summer, while ΣH_2S had a mid-depth maximum of 15–22 $\mu mol \cdot L^{-1}$ during the summer (Fig. 1). pH varied from 6.2 to 6.6 during 1979.

Davison and Heaney (1978) observed a mid-depth ΣH_2S maximum in Esthwaite Water that is similar to those in L227. They attributed this profile shape to amorphous FeS formation. Solubility calculations were made to determine whether FeS is limiting the ΣH_2S concentration in L227 (Fig. 1).

The p(IAP) values (Fig. 1) reached a minimum at the depth where ΣH_2S is a maximum. Below this depth Fe^{2+} concentrations increased and ΣH_2S concentrations decreased, while the p(IAP) values remained constant. The behavior of these three parameters signifies the formation of a FeS phase. At depths shallower than the ΣH_2S maximum the lake was undersaturated with respect to FeS. Increases in ΣH_2S and Fe^{2+} with depth caused saturation for FeS at the depth where ΣH_2S is a maximum. Further increases in Fe^{2+} limited the concentration

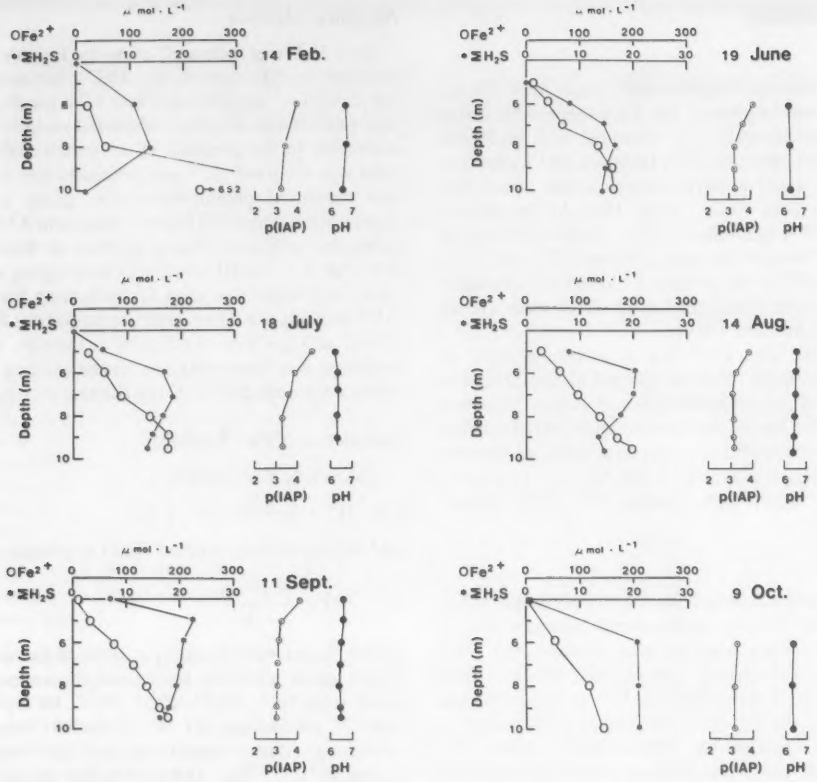


FIG. 1. ΣH_2S (*), Fe^{2+} (○), and pH (●) in the hypolimnion of L227 in 1979. ⊙, p(IAP) values calculated from pH, ΣH_2S, and Fe^{2+} (see text).

of ΣH_2S in accord with reaction 1. At the depth of maximum ΣH_2S concentration and below, the p(IAP) equalled the solubility product constant (pK_{sp}) for FeS.

The average pK_{sp} in 1979 was 3.16 (Table 1). Although there was a slight variation in temperature during this period, there is no correlation between temperature and pK_{sp}. This is due to a combination of the small ΔH^0 for FeS (-2 kcal·mol^{-1} (8.4 kJ·mol^{-1}), Smith and Martell 1976) and the analytical uncertainty of the ΣH_2S, Fe^{2+}, and pH measurements.

Davison (1980) made a critical comparison of FeS solubility in natural waters. Using data in which either particulate FeS was found to be in equilibrium with Fe^{2+} and ΣH_2S or data that had a mid-depth maximum in ΣH_2S, Davison showed that seasonally anoxic systems have pK_{sp} values that are close to the laboratory-determined value for freshly precipitated amorphous FeS. Systems that have longer periods of anoxia, such as the Black Sea, have a more aged FeS precipitate that has been mineralized into the more stable mackinawite form. This is in agreement with Berner (1967) who argued that, on the basis of Gibbs free energy, amorphous FeS in the presence of elemental sulfur is metastable, eventually reacting to form, in sequence, mackinawite, greigite, and then pyrite.

pK_{sp} values for seasonally anoxic, freshwater systems from Davison's work (Table 2) are in the range 2.59–3.25 and span the average value determined for L227 in 1979, as well as earlier data for L227 and nearby ELA L223 (Cook 1981). These values are all similar to the laboratory-determined p(IAP) of 2.87 at 4°C (Berner 1967). It should be noted that Davison (1980) used a value of $10^{-7.42}$ for the first dissociation constant for H_2S rather than $10^{-7.25}$ used in this study. Taking $pK_1 = 7.42$ would change the values in L227 from 3.16 to 3.31, which is at the upper range for Davison's data set.

Sediments

In the interstitial water samples collected on 28 August 1979 at a depth of 10 m, Fe^{2+} exhibited a steep gradient in the first 10 cm and then slowly increased to 1000 μmol·L^{-1} at 40 cm (Fig. 2). ΣH_2S was measurable in the top 10 cm but was less than the detection limit below that depth. pH was a uniform 6.45 in the top 50 cm.

AVS concentrations from the core (Table 3) were at a maximum in the top 10 cm and decreased to 1 μmol·g^{-1} at 20 cm. The core was black to 8 cm, changed from black to brown in the zone 8–12 cm, and was uniformly brown below that depth. Water content decreased from 99% at the surface to 95% at 15 cm (Table 3). Total iron concentrations were around 500 μmol·g^{-1} and exhibited little trend (Table 3). Mossbauer spectroscopy measurements by Coey et al. (1974) indicated that ferric hydroxide (major phase) and chlorite and illite (minor phases) were present and that magnetic Fe minerals were absent from L227 sediments. The dried surface sediments in L227 are 48.5% organic matter (Brunskill et al. 1971).

Ion activity calculations, made using activity coefficients

TABLE 1. pK_{sp} for FeS at and below the mid-depth ΣH_2S maximum in L227 in 1979. Winter temperatures are estimated.

Date	z (m)	pK_{sp}	Temperature (°C)
14 Feb.	8	3.32	(4)
	10	3.02	(4)
19 June	8	3.26	4.24
	10	3.20	4.20
18 July	8	3.28	4.31
	9	3.34	4.22
	9.5	3.28	4.21
14 Aug.	6	3.22	5.09
	7	3.12	5.03
	8	3.10	5.03
	9	3.12	4.43
	9.5	3.10	4.41
11 Sept.	5	3.32	5.99
	6	3.14	5.00
	7	3.06	4.64
	8	3.08	4.53
	9	2.98	4.51
	9.5	3.06	4.51
9 Oct.	6	3.38	5.41
	8	3.20	4.81
	9.5	3.10	4.65
Average		3.16 ±0.12	4–6

from the water column at 10 m on 14 August 1979, reveal that the pore waters in L227 are in equilibrium with amorphous FeS in the top 10 cm and with mackinawite at 12 cm (Fig. 3). Below 12 cm, p(IAP) is determined using the ΣH_2S detection limit (0.4 $\mu mol \cdot L^{-1}$) and is a lower limit. AVS exists in the sediment down to 25 cm (Table 3) and, based on the solubility relationships, may be greigite.

FeS may be transformed into pyrite (FeS_2). Rickard (1975) demonstrated that the transformation of FeS to pyrite involves the dissolution of S^0 to form polysulfides, and FeS to produce Fe^{2+}. These two species then react to form pyrite. A mechanism for the direct precipitation of pyrite from Fe^{2+} and ΣH_2S has also been proposed (Howarth 1979), although this mechanism appears to be important only at pHs lower than those in L227 (Berner et al. 1979). The existence of trace amounts of pyrite in the top 20 cm of sediment in L227 was confirmed by Mossbauer spectroscopy (Coey et al. 1974) and by scanning electron microscopy coupled with energy-dispersive X-ray fluorescence spectroscopy (Cook 1981), although pyrite abundance was not quantified in either study.

The AVS distribution in L227 sediments (Table 3) was the result of diagenetic processes and the supply of sulfate. The seasonal cycle of anoxia followed by overturn dictates that SO_4^{2-} was supplied to the hypolimnion only at overturn. This SO_4^{2-} was reduced at the sediment–water interface to ΣH_2S, which then reacted with Fe^{2+} to form FeS. Because the high values of Fe^{2+} limit the ΣH_2S to low concentrations, little ΣH_2S can diffuse to deeper in the sediments, and FeS is maximum in the upper 10 cm. Additional FeS might settle out of the water column onto the sediments. The breakdown of sulfur-containing amino acids is a negligible source of sulfide in L227 (Cook 1981).

The FeS distribution may also be the result of the experimental eutrophication. Although sulfide and Fe^{2+} measurements were not made before the experiment, AVS probably formed in L227 because several months of anoxia per year are common in small lakes in the area due to incomplete spring and fall mixing. Lake 383, an unfertilized natural ELA lake with a surface area and maximum depth almost identical to L227, exhibited a mid-depth maximum in ΣH_2S concentration, and presumably, FeS formation took place in 1974 (D. W. Schindler, unpubl. data). After the experimental eutrophication, the hypolimnion of L227 became more anoxic, with the production of more ΣH_2S, Fe^{2+}, and FeS, which accumulated in the surface sediments. Lake Mendota (Wisconsin) has a similar AVS peak in the surface sediments that was attributed to a greater degree of primary production and hypolimnion oxygen deficit, brought on by human activities in the watershed (Nriagu 1968).

The dissolved inorganic carbon (DIC) concentrations of the pore waters in L227 sediments measured in 1975 and 1979 (Hesslein 1976b; C. A. Kelly, Freshwater Institute, Winnipeg, Man., unpubl. data) had an exponential profile (i.e. $1 - \exp(-az)$) similar to that for Fe^{2+}, with values increasing from 1.0 $mmol \cdot L^{-1}$ at the sediment–water interface to 2.8 $mmol \cdot L^{-1}$ at a depth of 20 cm. Saturation calculations for siderite ($FeCO_3$) using

$$Fe^{2+} + CO_3^{2-} \rightleftarrows FeCO_3$$

and using activity coefficients determined as for sulfide indicate

TABLE 2. pK_{sp} for laboratory measurements and other lakes.

Locality	Year	pK_{sp}	Temperature (°C)	pH	Reference
L227	1979	3.16	4–6	6.5	This work
L227	1974–78	3.16	4–6	6.5	Cook 1981
L223	1977–79	3.08	6–8	6.5	Cook 1981
Esthwaite Water	—	2.59	10	7.13	Davison 1980
Abereiddy Quarry	—	2.94	10	7.17	Davison 1980
Clear Lake	—	3.25	8	6.9	Davison 1980
Laboratory (amorphous FeS)	—	2.97(2.87)[a]	25(4)[a]	3.7	Berner 1967
Laboratory (greigite)	—	4.30(4.10)[a]	25(4)[a]	3	Berner 1967
Laboratory (mackinawite)	—	3.75(3.65)[a]	25(4)[a]	4	Doyle 1968

[a]Estimated from ΔH^0 for FeS (Smith and Martell 1976) and the pK_{sp} value at 25°C.

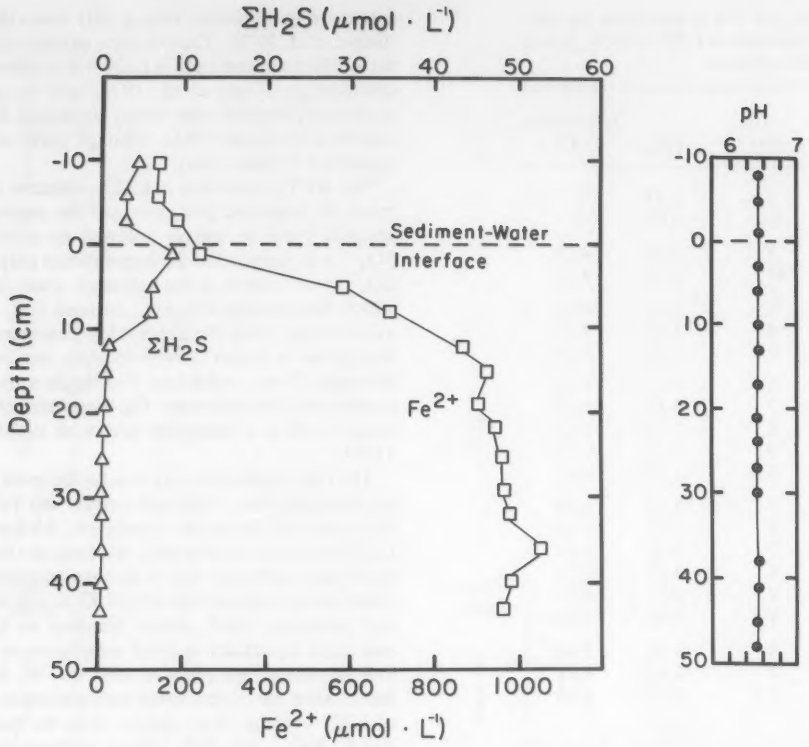


FIG. 2. ΣH_2S (△), Fe^{2+} (□), and pH (●) in the pore water at 10 m in L227. Sampled on 28 August 1979.

TABLE 3. Sediment chemistry from a core taken at 9 m in August 1979 in L227. Concentrations are per gram dry weight.

Depth (cm)	H_2O (%)	AVS ($\mu mol \cdot g^{-1}$)	Fe ($\mu mol \cdot g^{-1}$)
0–1	98.9	41	449
1–2	97.4	77	578
2–3	97.4	88	507
3–4	97.2	92	523
4–5	97.4	62	519
5–6	97.2	28	587
6–7	96.4	30	627
7–8	95.8	14	535
8–9	95.6	9	444
9–10	95.4	7	457
15–16	94.8	3	452
20–21	95.4	2	507
25–26	95.1	1	421

that the ion activity product at 0 cm was 19% of the theoretical value of K_{sp} ($10^{-10.5}$ at 4°C, Berner 1971), while that at 20 cm was 214%. Therefore, where the pore water and sediments have relatively high ΣH_2S and AVS concentrations, the pore waters are undersaturated with siderite. Where the pore water and sediments have low ΣH_2S and AVS concentrations the pore waters are supersaturated with siderite.

Siderite is stable only in sediments that have low ΣH_2S and high Fe^{2+} pore water concentrations (Berner 1971). The existence of siderite has also been predicted in other low ΣH_2S systems: Linsley Pond, CT (Doyle 1967), Greifensee (Emerson 1976), ELA Lake 120 (Campbell and Torgersen 1980), and Lake Vechten (Verdouw and Dekkers 1980). The low-sulfur sediments of a freshwater swamp, which were supersaturated with respect to siderite, had measurable siderite concentrations (Postma 1982).

The Fe^{2+} pore water profiles in L227 appear to be governed by two precipitation reactions (FeS and $FeCO_3$), as well as production and diffusion. The production of Fe^{2+} is probably the result of organic matter oxidation with iron (III) hydroxide acting either as a direct or indirect electron acceptor (Froelich et al. 1979; Sorenson 1982). The low concentrations at the top of the profile are the result of diffusive loss into the water column and FeS saturation with the relatively high ΣH_2S concentrations in this zone. The constant, high values of Fe^{2+} at depths greater than 12 cm in the sediment may be the result of (1) saturation with FeS at low values of ΣH_2S, (2) Fe^{2+} production from iron (III) hydroxide via the oxidation of organic matter (Sorenson 1982), and (3) saturation with $FeCO_3$. The shape of the profile (concave downward) suggests that production of Fe^{2+} is more important than uptake by reaction with carbonate, which would yield a profile that is concave upwards. Similar concave downward profiles that have constant, high concentrations at depth are observed for other solutes produced during diagenesis of organic matter (Berner 1980).

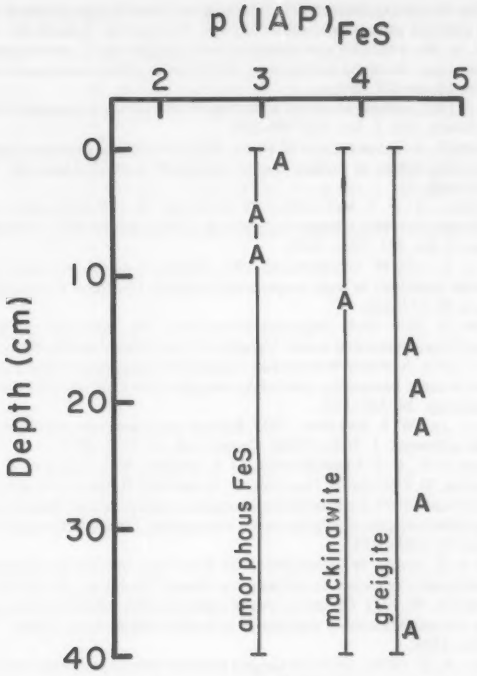


FIG. 3. Ion-activity products (A) for the pore water data from Fig. 2.

Iron Flux from Sediments

Pore-water profiles provide information on the gradient at the sediment–water interface $(\partial C/\partial z)_0$, which, along with the diffusion coefficient (D), yields an estimate of the iron (II) flux (F) via

$$F = -\frac{\Phi}{\theta^2} D \left(\frac{\partial C}{\partial z}\right)_0 = -\Phi D_s \left(\frac{\partial C}{\partial z}\right)_0$$

where Φ is the porosity, θ is the tortuosity, and D_s is the bulk diffusion coefficient.

Hesslein's (1980) in situ determination of the pore water diffusion coefficient for tritiated water provides a means of estimating the bulk diffusion coefficient of Fe^{2+}. Taking the ratio of the measured diffusion coefficient for tritiated water in L227 sediments ($0.5 \times 10^{-5}\,cm^2 \cdot s^{-1}$) to the self-diffusion coefficient reported by Wang et al. (1953) and multiplying by the Fe^{2+} molecular diffusion coefficient (Li and Gregory 1974) yields $1.5 \times 10^{-6}\,cm^2 \cdot s^{-1}$ for D_s.

Using the pore water Fe^{2+} gradient between 0 and 5 cm ($80\,\mu mol \cdot L^{-1} \cdot cm^{-1}$) the flux is $0.1\,mmol \cdot m^{-2} \cdot d^{-1}$. Because of the increase in Fe^{2+} in the water column during the year (Fig. 1), the gradient at the sediment–water interface varies from a maximum after overturn to a minimum prior to an overturn. The use of an August pore water profile should represent an average gradient. Hesslein (1976b), on the basis of a non-steady-state diagenetic model for NH_4^+, CH_4, and DIC, showed that the pore water gradient does not vary by more than a factor of two over the period of anoxia. Therefore, the Fe^{2+} flux probably ranged from approximately 0.065 to $0.130\,mmol \cdot m^{-2} \cdot d^{-1}$ during the year.

A more direct estimate of flux from the sediments may be obtained from the observed linear increase in hypolimnion Fe^{2+} mass with time during summer stagnation ($25\,mol \cdot d^{-1}$) and the sediment area from which the Fe^{2+} is diffusing ($2.3 \times 10^4\,m^2$); this results in $1.1\,mmol \cdot m^{-2} \cdot d^{-1}$, which is 11 times the pore water flux. Therefore, over 90% of the observed flux must come from a location other than the pore water, and the probable location is the sediment–water interface. This finding is comparable with that of Hesslein (1976b), who demonstrated on the basis of a similar study that only 10% of the observed flux of NH_4^+, CH_4, and DIC could be accounted for by pore water processes below the top 1 cm of sediment. Enhancement of the pore water flux due to ebullition (Klump and Martens 1981) was not a factor because the total partial pressure of gases was less than the hydrostatic pressure (Hesslein 1976b). Hesslein concluded that the pore water gradient was much steeper due to production in the upper few millimetres of sediment. Therefore, the spatial resolution of the pore water sampler is not sufficient to determine the gradient; the observed gradient and the resulting flux is only a lower limit. According to Kipphut's (1978) estimate of L227 sedimentation rate ($0.9\,mm \cdot yr^{-1}$) the upper 1 cm of sediment is less than 10 yr old. Hesslein (1976b) inferred that this production at the sediment–water interface represents decomposition of recently deposited material, while pore water flux represents decomposition of older materials.

The importance of the sediment–water interface was shown by Murray and Gill (1978), who reported that Fe^{2+} diffusion out of the pore water, as determined by pore water gradients, could not support the existing water column concentration of acid-soluble iron in Puget Sound. They suggested that the flux is derived from processes at sediment depths shallower than 0.4 cm that were not resolvable by their sampling techniques. Davison et al. (1981) showed that the water column burden of iron in Esthwaite Water could be predicted from the benthic-boundary-layer gradient and proposed that this flux is derived from the sediment–water interface.

Values for Fe^{2+} flux from sediments in several locations range from a low of $0.18\,mmol \cdot m^{-2} \cdot d^{-1}$ reported in Lake Erie to $40\,mmol \cdot m^{-2} \cdot d^{-1}$ in ELA Lake 223 (Table 4).

The Fe^{2+} in the water column meets one of three fates: (1) diffuses to the oxic–anoxic interface at 4 m and undergoes oxidation, (2) forms iron sulfide minerals, or (3) remains in the anoxic hypolimnion until an overturn when it will be oxidized. The small rate of mixing at the base of the thermocline (4 m) (Quay et al. 1980) confines Fe^{2+} to the hypolimnion until overturn, when the Fe^{2+} is oxidized. The concentration of Fe^{2+} is not affected by FeS formation (Fig. 1). Thus, the latter fate is the most important in L227. Experimental work indicates that chemical oxidation of Fe^{2+} has a half-life of less than 3 h and yields an iron (III) hydroxide (Sung and Morgan 1980; Davison and Seed 1983). This solid phase then settles out of the water column and onto the sediment surface. During the next period of anoxia, this iron (III) hydroxide at the sediment–water interface is reduced and diffuses into the water column.

The net iron sedimentation rate was $0.07\,mmol \cdot m^{-2} \cdot d^{-1}$ based on a sedimentation rate of $0.9\,mm \cdot yr^{-1}$ (Kipphut 1978), the iron concentration of $500\,\mu mol \cdot g^{-1}$ (dry), and the water content (Table 3). For steady state to be maintained in the sediments, the total sedimentation rate of iron should be $1.17\,mmol \cdot m^{-2} \cdot d^{-1}$ of which $1.0\,mmol \cdot m^{-2} \cdot d^{-1}$ was reduced and redissolved at the sediment–water interface, $0.1\,mmol \cdot m^{-2} \cdot d^{-1}$ was reduced in the upper 10 cm of sediment, and $0.07\,mmol \cdot m^{-2} \cdot d^{-1}$ accumulated in the sediments. Thus, 94%

TABLE 4. Fe^{2+} flux from anoxic sediments.

System	Flux ($mmol \cdot m^{-2} \cdot d^{-1}$)	Reference
L227	1.1	This work
Esthwaite Water	0.31–3.46	Davison et al. 1981
Puget Sound	0.73	Murray and Gill 1978
L223	40	Cook 1981
Laboratory	1.57	Fillos and Swanson 1975
Baltic Sea	0.73	Balzer 1982
Lake Erie	0.18–0.39	Adams et al. 1982

of the iron reaching the sediments was recycled back into the water column and 6% was removed from the cycle. To maintain steady state for the whole lake the allochthonous inputs of iron must be of the order of 0.07 $mmol \cdot m^{-2} \cdot d^{-1}$.

Acknowledgments

This work has profited from discussions with W. S. Broecker, R. H. Hesslein, R. A. Berner, P. Santschi, Y.-H. Li, T. C. Johnson, and D. W. Schindler. J. Penny and J. Prokopowich supervized sampling and chemical analyses. Thanks to A. Hedin and P. Catanzaro for manuscript preparation. Financial support was provided by NSF grants OCE-78-20898, DAR-79-17291, and DEB-80-17639.

References

ADAMS, D. D., G. MATISOFF, AND W. J. SNODGRAS. 1982. Flux of reduced chemical constituents (Fe^{2+}, Mn^{2+}, NH_4^+, and CH_4) and sediment oxygen demand in Lake Erie. Hydrobiologia 92: 405–414.

BALZER, W. 1982. On the distribution of iron and manganese at the sediment–water interface: thermodynamic versus kinetic control. Geochim. Cosmochim. Acta 46: 1153–1161.

BERNER, R. A. 1967. Thermodynamic stability of sedimentary iron sulfides. Am. J. Sci. 265: 773–785.

1971. Principles of chemical sedimentology. McGraw-Hill, New York, NY. 240 p.

1980. Early diagenesis: a theoretical approach. Princeton University Press, Princeton, NJ. 237 p.

BERNER, R. A., T. BALDWIN, AND G. R. HOLDREN. 1979. Authigenic iron sulfide as paleosalinity indicators. J. Sediment. Petrol. 49: 1345–1350.

BLACK, C. A. 1965. Methods of soil analysis. Part 2. Chemical and microbiological properties. University of Wisconsin Press, Madison, WI. 388 p.

BRUNSKILL, G. J., D. PAVOLEDO, B. W. GRAHAM, AND M. P. STAINTON. 1971. Chemistry of surface sediments of sixteen lakes in the Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Board Can. 28: 277–294.

BRUNSKILL, G. J., AND D. W. SCHINDLER. 1971. Geography and bathymetry of selected lake basins, Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Board Can. 28: 139–155.

CAMPBELL, P., AND T. TORGERSEN. 1980. Maintenance of iron meromixis by iron redeposition in a rapidly flushed monimolimnion. Can. J. Fish. Aquat. Sci. 37: 1303–1313.

COEY, J. M. D., D. W. SCHINDLER, AND F. WEBER. 1974. Iron compounds in lake sediments. Can. J. Earth Sci. 11: 1489–1493.

COOK, R. B. 1981. The biogeochemistry of sulfur in two small lakes. Ph.D. dissertation, Columbia University, New York, NY. 248 p.

DAVISON, W. 1980. A critical comparison of measured solubilities of ferrous sulfide in natural waters. Geochim. Cosmochim. Acta 44: 803–808.

1981. Supply of iron and manganese to an anoxic lake basin. Nature (London) 290: 241–243.

DAVISON, W., AND S. I. HEANEY. 1978. Ferrous iron sulfide interactions in anoxic hypolimnetic waters. Limnol. Oceanogr. 23: 1194–1200.

DAVISON, W., S. I. HEANEY, J. F. TALLING, AND E. RIGG. 1981. Seasonal transformations and movements of iron in a productive U.K. lake with deep-water anoxia. Schweiz. Z. Hydrol. 42: 196–224.

DAVISON, W., AND G. SEED. 1983. The kinetics of the oxidation of ferrous iron in synthetic and natural waters. Geochim. Cosmochim. Acta 47: 67–79.

DOYLE, R. W. 1967. Eh and thermodynamic equilibrium in environments containing dissolved ferrous iron. Ph.D. dissertation, Yale University, New Haven, CT. 100 p.

1968. Identification and solubility of iron sulfide in anaerobic lake sediment. Am. J. Sci. 266: 980–994.

DUCHART, P., S. CALVERT, AND N. PRICE. 1973. Distribution of trace metals in the pore waters of shallow marine sediments. Limnol. Oceanogr. 18: 605–610.

ELDERFIELD, H., R. J. MCCAFFREY, N. LUEDTKE, M. BENDER, AND V. A. TRUESDALE. 1981. Chemical diagenesis in Narragansett Bay sediments. Am. J. Sci. 281: 1021–1055.

ELLIS, A. J., AND W. GIGGENBACH. 1971. Hydrogen sulfide ionization and sulfur hydrolysis in high temperature solutions. Geochim. Cosmochim. Acta 35: 247–260.

EMERSON, S. 1976. Early diagenesis in anaerobic lake sediments: chemical equilibria in interstitial waters. Geochim. Cosmochim. Acta 40: 925–934.

FEE, E. J. 1979. A relation between lake morphometry and primary productivity and its use in interpreting whole-lake eutrophication experiments. Limnol. Oceanogr. 24: 401–416.

FILLOS, J., AND W. R. SWANSON. 1975. Release rate of nutrients from river and lake sediments. J. Water Pollut. Control Fed. 47: 1032–1042.

FROELICH, P. N., G. P. KLINKHAMMER, M. L. BENDER, N. A. LUEDKTE, G. R. HEATH, D. CULLEN, P. DAUPHIN, D. HAMMOND, B. HARTMAN, AND V. MAYNARD. 1979. Early oxidation of organic matter in pelagic sediments of the eastern equatorial Atlantic: suboxic diagenesis. Geochim. Cosmochim. Acta 43: 1075–1090.

GIBLIN, A. E., AND R. W. HOWARTH. 1983. Pore water evidence for a dynamic sedimentary iron cycle in salt marshes. Limnol. Oceanogr. 28: 70–82.

GIGGENBACH, W. 1971. Optical spectra of highly alkaline sulfide solutions and the second dissociation constant of hydrogen sulfide. Inorg. Chem. 10: 1333–1338.

HESSLEIN, R. H. 1976a. An *in situ* sampler for close interval pore water studies. Limnol. Oceanogr. 21: 912–914.

1976b. The fluxes of CH_4, CO_2, and NH_3-N from sediments and their consequent distribution in a small lake. Ph.D. dissertation, Columbia University, New York, NY. 186 p.

1980. In situ measurements of pore water diffusion coefficients using tritiated water. Can. J. Fish. Aquat. Sci. 37: 545–551.

HOWARTH, R. W. 1979. Pyrite: its rapid formation in a salt marsh and its importance in ecosystem metabolism. Science (Washington, DC) 203: 49–51.

JOHNSON, W. E., AND J. R. VALLENTYNE. 1971. Rationale, background, and development of experimental lake studies in northwestern Ontario. J. Fish. Res. Board Can. 28: 123–128.

KIPPHUT, G. W. 1978. An investigation of sedimentary processes in lakes. Ph.D. dissertation, Columbia University, New York, NY. 180 p.

KLUMP, J. V., AND C. S. MARTENS. 1981. Biogeochemical cycling in an organic rich coastal marine basin — II. Nutrient sediment–water exchange processes. Geochim. Cosmochim. Acta 45: 101–121.

LI, Y.-H., AND S. GREGORY. 1974. Diffusion of ions in sea water and in deep-sea sediments. Geochim. Cosmochim. Acta 38: 703–714.

MURRAY, J. W., AND G. GILL. 1978. The geochemistry of iron in Puget Sound. Geochim. Cosmochim. Acta 42: 9–19.

NRIAGU, J. 1968. Sulfur metabolism and sedimentary environment: Lake Mendota, Wisconsin. Limnol. Oceanogr. 13: 430–439.

POSTMA, D. 1982. Pyrite and siderite formation in brackish and freshwater sediments. Am. J. Sci. 282: 1151–1183.

PRESLEY, B., Y. YOLODNY, A. NISSENBAUM, AND I. R. KAPLAN. 1972. Early diagenesis in a reducing fjord, Saanich Inlet, British Columbia, II. Trace element distribution in interstitial water and sediment. Geochim. Cosmochim. Acta 36: 1073–1090.

QUAY, P. D., W. S. BROECKER, R. H. HESSLEIN, AND D. W. SCHINDLER. 1980. Vertical diffusion rates determined by tritium tracer experiments in the thermocline and hypolimnion of two lakes. Limnol. Oceanogr. 25: 201–218.

RICKARD, D. T. 1975. Kinetics and mechanism of pyrite formation at low temperatures. Am. J. Sci. 275: 636–652.

SCHINDLER, D. W. 1971. Light, temperature, and oxygen regimes of selected lakes in the Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Board Can. 28: 157–169.

1975. Whole-lake eutrophication experiments with phosphorous, nitrogen, and carbon. Verh. Int. Ver. Limnol. 19: 3221–3231.

SCHINDLER, D. W., H. KLING, R. V. SCHMIDT, J. PROKOPOWICH, V. E. FROST, R. A. REID, AND M. CAPEL. 1973. Eutrophication of Lake 227 by addition of phosphate and nitrate: the second, third, and fourth years of

enrichment, 1970, 1971, and 1972. J. Fish. Res. Board Can. 30: 1415–1440.

SMITH, P. M., AND A. E. MARTELL. 1976. Critical stability constants. Vol. 4. Inorganic complexes. Plenum Press, New York, NY.

SORENSON, J. 1982. Reduction of ferric iron in anaerobic, marine sediment and interaction with reduction of nitrate and sulfate. Appl. Environ. Microbiol. 43: 319–324.

SPENCER, D. W., AND P. G. BREWER. 1971. Vertical advective diffusion and redox potentials as controls on the distribution of manganese and other trace metals dissolved in waters of the Black Sea. J. Geophys. Res. 76: 5877–5892.

STAINTON, M. P., M. J. CAPEL, AND F. A. J. ARMSTRONG. 1977. The chemical analysis of freshwater. 2nd ed. Fish. Res. Board Can. Misc. Spec. Publ. 25: 166 p.

STUMM, W., AND J. J. MORGAN. 1981. Aquatic chemistry. 2nd ed. Wiley-Interscience, New York, NY. 780 p.

SUNG, W., AND J. J. MORGAN. 1980. Kinetics and products of ferrous iron oxygenation in aqueous systems. Environ. Sci. Technol. 14: 561–568.

VERDOUW, H., AND E. M. J. DEKKERS. 1980. Iron and manganese in Lake Vechten (The Netherlands): dynamics and role in the cycle of reducing power. Arch. Hydrobiol. 89: 509–532.

WANG, J. H., C. V. ROBINSON, AND I. S. EDELMAN. 1953. Self-diffusion and structure of liquid water. III. Measurement of the self-diffusion of liquid water with H^2, H^3, and O^{18} as tracers. J. Am. Chem. Soc. 75: 466–470.

Ichthyoplankton Associated with a Warm Core Ring off the Scotian Shelf

J. S. Wroblewski and Jerry Cheney

Department of Oceanography, Dalhousie University, Halifax, N.S. B3H 4J1

Wroblewski, J. S., and J. Cheney. 1984. Ichthyoplankton associated with a warm core ring off the Scotian Shelf. Can. J. Fish. Aquat. Sci. 41: 294–303.

A warm core ring and adjacent waters off the Scotian Shelf in June 1982 contained substantial numbers of larval and juvenile white hake, *Urophycis tenuis*, as far as 140 km seaward of the continental shelf break. The warm core ring, designated 81-G, had entrained shelf water on several occasions before the shipboard observations were made. We suggest that the ring contributed to the offshore advection of these fish, which probably were spawned on the continental shelf or upper slope. Warm core rings can disrupt the usual larval drift pattern of shelf–slope fishes and thereby affect recruitment. Larvae and juveniles of several species of tropical–subtropical fishes found in ring 81-G have been reported previously as rare specimens in ichthyoplankton surveys on the Scotian Shelf. Our observations support the hypothesis that warm core rings can be a mechanism for transport of these expatriated fishes onto the shelf.

Un anneau à cœur chaud ainsi que les eaux avoisinantes au large du plateau Scotian contenaient, en juin 1982, des nombres substantiels de larves et de jeunes merluches blanches, *Urophycis tenuis*, aussi loin que 140 km au large de la marge du plateau continental. Cet anneau, désigné comme 81-G, avait entraîné de l'eau du plateau en plusieurs occasions avant qu'eurent été faites des observations à bord d'un navire. Nous avançons l'hypothèse que cet anneau a contribué à l'advection au large de ces poissons, qui avaient été probablement pondus sur le plateau continental ou à la partie supérieure de la pente. Des anneaux à cœur chaud peuvent déranger la dérive larvaire usuelle des poissons du plateau et de la pente continentale et, partant, influencer le recrutement. Les larves et les juvéniles de plusieurs espèces de poissons tropicaux–subtropicaux ont été trouvés dans l'anneau 81-G, et ont été déjà signalés comme rares dans les relevés ichtyoplanctoniques du plateau Scotian. Nos observations confirment l'hypothèse que les anneaux à cœurs chaud peuvent être un mécanisme de transport de ces poissons expatriés sur le plateau.

Received July 8, 1983
Accepted October 28, 1983

Reçu le 8 juillet 1983
Accepté le 28 octobre 1983

Accounts of the influence of warm core Gulf Stream rings on the distribution of fish larvae on the continental shelf off the eastern United States and Canada have appeared in recent literature (Markle et al. 1980) and in newsletters (Maurer et al. 1979; Friedlander and Smith 1983). G. R. Flierl and J. S. Wroblewski (unpubl. manuscr.) modeled the potential impact of warm core rings on larval fish distributions over the continental shelf off the northeastern United States. Their model suggested that the offshore flows associated with a ring can transport larvae of shelf fishes beyond the shelf break in an entrainment feature behind the ring. As the first observational evidence of this process, Friedlander and Smith (1983) reported larvae of the sand lance (*Ammodytes* sp.) from an entrainment feature of a ring off New Jersey.

Onshore flows that occur ahead of the anticyclonically rotating eddy can transport fish larvae of warmer water origin onto the shelf. Markle et al. (1980) discovered fish larvae of subtropical and tropical origin on the Scotian Shelf and attributed their presence to warm core ring activity. Maurer et al. (1979) observed slope water forms of copepods, chaetognaths, and larvae of the red hake, *Urophycis chuss*, over the continental shelf off southern New England and inferred that their occurrence was due to a warm core ring. Sea surface temperature maps derived from satellite imagery showed that a ring was present at the shelf edge at the time of their observations.

To investigate these processes more closely, we surveyed a warm core ring off the Scotian Shelf to identify the ichthyoplankton associated with the ring and the surrounding shelf and slope water. In addition to collecting temperature and salinity data, we also identified the chaetognaths from this survey to determine the origins of the water sampled.

Materials and Methods

Warm core ring (WCR) 81-G formed in early December 1981 from a large Gulf Stream meander centered at 39.8°N, 62.5°W (Fitzgerald and Chamberlin 1982) (Fig. 1). The ring had undergone three major interactions with the Gulf Stream (during the weeks of 1 February, 15 March, and 24 May 1982) and had entrained shelf water off the Scotian Shelf on several occasions (during the weeks of 29 March, 19 April, 3 May, and 10 May) (Fig. 2). These events made the ring a good candidate for our investigation.

Samples were collected on C.S.S. *Dawson* cruise No. 82016 during the period 5–7 June 1982. Ocean frontal analysis charts provided by the U.S. National Weather Service–National Earth Satellite Service were used to locate the ring, and updated ring coordinates were transmitted to us by personnel at the Bedford Institute of Oceanography. Sampling consisted of underway surface salinity, temperature, and in vivo fluorometry measurements using the ship's seawater intake about 1 m below the

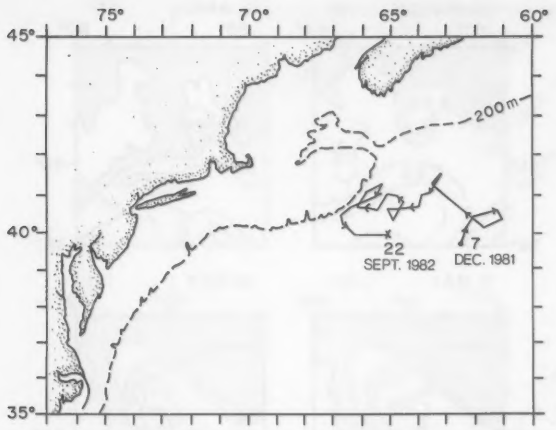


FIG. 1. Trackline of 81-G ring center positions from ring formation (7 Dec. 1981) to its destruction (22 Dec. 1982) (courtesy of Atlantic Environmental Group, U.S. National Marine Fisheries Service).

surface. Details of these sampling methods are presented by Fournier et al. (1984). In vitro surface chlorophyll *a* concentration was determined from discrete samples taken from the seawater intake every 0.5 h. Continuous-flow in vivo fluorometry values were used to interpolate between the 0.5-h in vitro chlorophyll samples, taking into account changes in the chlorophyll to phaeophytin ratio.

A total of 24 stations were occupied in the ring vicinity and interior. A transect was made into WCR 81-G from the northeast, then stations were occupied within the ring, and finally a transect was run across the ring on a northwest heading (Fig. 3). At individual stations, expendable bathythermograph (XBT) profiles were taken, and bucket temperature and salinity measurements were made. Both neuston and bongo nets were towed at 14 stations. The 333-μm mesh bongo net was towed obliquely from the surface to a depth of approximately 100 m and back again to the surface. The depth of the tow was estimated from the wire angle and length of wire out. The 1-m-wide neuston net with 333-μm mesh was towed at the surface simultaneously with the bongo net deployment. Tow times were usually of 30- to 45-min duration and each bongo net filtered between 311 and 656 m^3, as determined from flowmeters in the mouth of each net. Samples from both the right and left bongo nets were kept only for the first two tows, after which the samples from the left net were used for other purposes. Plankton samples were preserved in 4% buffered formalin–seawater solution. Either entire samples or aliquots (>1/32) were examined later in the laboratory for the presence of larval fishes and for chaetognaths to be used as water mass indicators.

All fishes were sorted from the neuston and bongo net samples and identified to species where possible. Chaetognaths were identified to species and enumerated only from the bongo net samples. Total number of fish and chaetognaths in each bongo net tow were converted to number per 1000 m^3. For the neuston net samples, fish larvae abundance was expressed as number per hour of tow.

Results

Hydrography

The areal distribution of sea surface temperature on 4 June as interpreted from surface temperature maps provided by the Hydrometeorology Division, Canadian Atmospheric Environment Service, from oceanographic frontal analysis charts provided by the U.S. National Weather Service, and from the continuous underway surface temperature traces and bucket temperatures at individual stations, is shown in Fig. 3. Shelf water (<10°C) extended for a considerable distance beyond the shelf break. Warm (>20°C) ring water had spread out at the surface giving the eddy a crescent shape in the frontal analysis charts.

The vertical distribution of temperature along the first transect clearly shows shelf water overlying slope water between stations 1 and 5 (Fig. 4). The shelf–slope front occurred between stations 5 and 6 where a plume of colder shelf water dipped below the surface. Stations 7 and 8 were near the edge of the crescent-shaped ring, which had partly enveloped the slope water at station 9. Highly variable surface temperatures and salinities (Fig. 5b and 5c) indicate that mixing of slope and ring water was occurring near the surface at stations 7 and 8. The ring edge was encountered at the surface between stations 10 and 11, where the 20°C isotherm broke the surface.

Anomalous depth of the 10°C isotherm is an indicator of subsurface warm core ring structure. Normally, in the slope water region where WCR 81-G was sampled, the 10°C isotherm occurs between 225 and 250 m depth (Fuglister 1963). In the ring the isotherm was considerably deeper (>300 m), indicative of the warm Sargasso Sea origin of the ring interior. The 10, 15, and 20°C isotherms (Fig. 4 and 6) map out the subsurface structure of WCR 81-G.

The crescent-shaped surface expression of the ring is again evident from the hydrographic section across the ring to the northwest. Ring water curled around shelf–slope water at station 12 and 75-m-thick tongue of warm ring water overlaid slope water at stations 13 and 14 (Fig. 6).

The lack of a thermostad or isothermal layer in the core of the ring might be expected of a ring that has undergone winter cooling. The original 18°C thermostad (Worthington 1976), which probably existed in the ring center when the eddy formed, must have lost a considerable amount of heat to the atmosphere during the winter of 1981–82. The 15°C isotherm probably shoaled from an initial depth of 600 m at the time of ring formation to an observed depth of 150 m when sampled in June (Fig. 4 and 6). A survey of ring 81-G during July 1982 also indicated the lack of a thermostad (D. Schink, Dep. of Oceanogr., Texas A&M Univ., pers. comm.).

Surface Chlorophyll Distributions

Frontal regions at the edge of WCR 81-G showed anomalously high surface chlorophyll values (Fig. 5a and 7a). These chlorophyll values were an order of magnitude higher than observed in the shelf and slope water and probably reflect increased nutrient availability in the frontal regions of the ring. No measurements of nutrient concentrations were made, but the raised isotherms at stations 9 and 12 may indicate that nutrient-rich deeper water was upwelled, permitting high local growth rates of the phytoplankton. Yoder et al. (1981) reported similar surface chlorophyll values in regions of upwelling associated with Gulf Stream frontal eddies off the southeastern continental shelf of the United States, but upwelling at the boundary of a warm core ring has not been previously reported. The low surface salinity at station 12 (Fig. 7) indicates some shelf water influence, but chlorophyll values at and near station

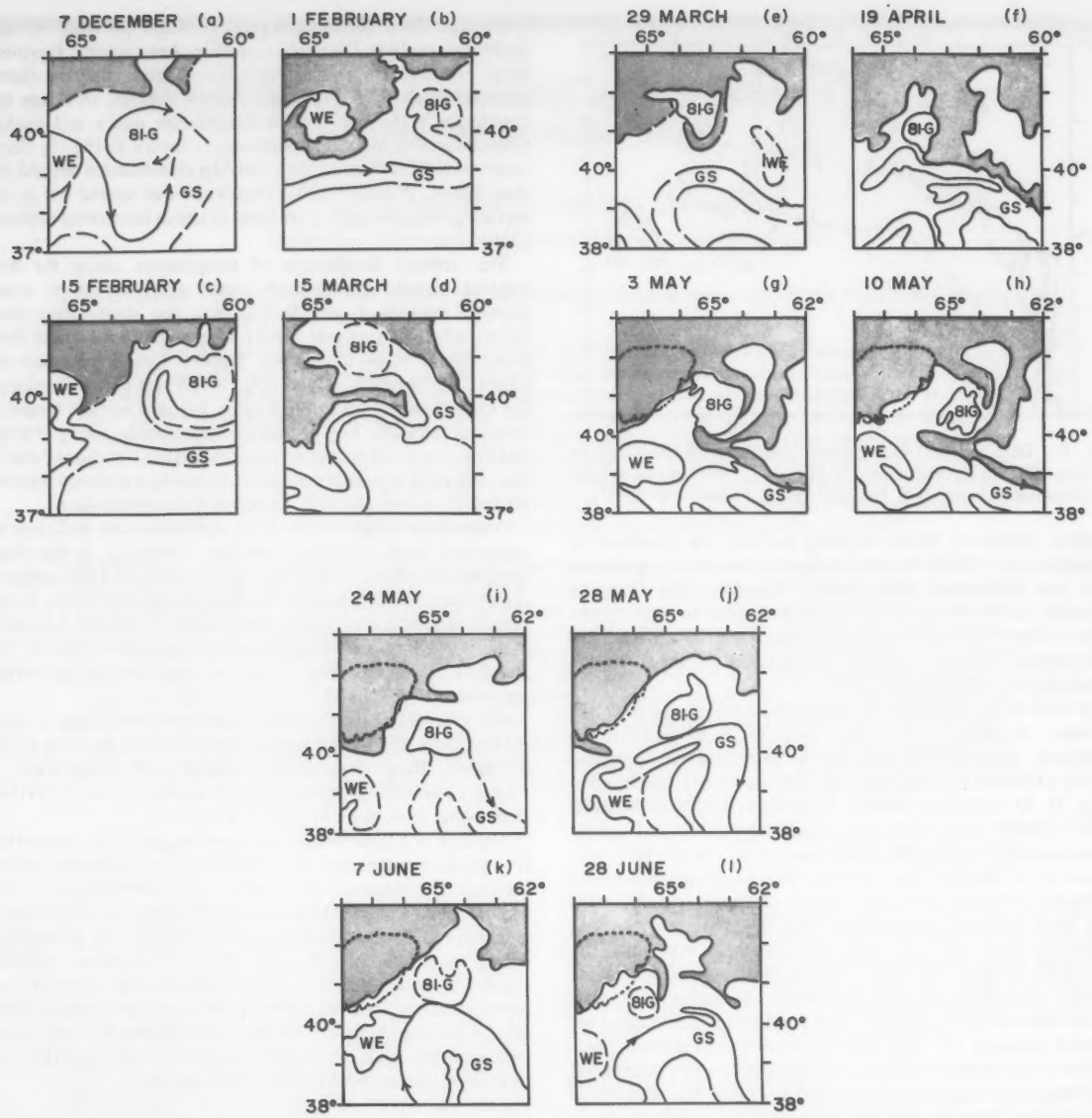


FIG. 2. Major events in the life history of 81-G interpreted from weekly oceanographic frontal analysis charts (U.S. National Weather Service–National Earth Satellite Service, modified by Atlantic Environmental Group, U.S. National Marine Fisheries Service). Shelf water is shaded. (a) Ring creation by pinching off of a Gulf Stream meander. Another warm eddy lies to the west. (b) Visible interaction with the Gulf Stream. (c) Visible streamer is attached from 81-G to the Gulf Stream. (d) Interaction of 81-G with northward meander of the Gulf Stream. Shelf water extends to the Gulf Stream. (e) 81-G entraining shelf water around itself. (f) Possible interaction with streamer from the Gulf Stream. Shelf water extends to the Gulf Stream. (g) 81-G moves closer to Georges Bank. Entrainment of shelf water is seen on northeast and southwest sides of the ring. (h) Influence of 81-G and the Gulf Stream on the shelf water continues. (i) Major interaction with the Gulf Stream occurs on the southern edge of 81-G. (j) 81-G appears separate from the Gulf Stream. Note the perturbation on the northeast edge of the ring. (k) 81-G appears crescent shaped. (l) 81-G entrains shelf water off Georges Bank and pushes slope water onto the Bank.

12 were much higher than at shelf water stations 1–3 (Fig. 5 and 7).

Chaetognath Distributions

To supplement the physical information on water masses in the study region, chaetognath abundance patterns were used as indicators of water type. Chaetognaths were chosen because their abundance patterns relative to hydrographic conditions in the slope water–northern Sargasso Sea region were recently described by Cheney (1982). The temperature, salinity, and chaetognath data together will aid in the interpretation of the data on larval fish distributions that follows.

Fifteen chaetognath species were identified from the 14 net tow stations (Table 1). *Sagitta elegans*, the only shelf water

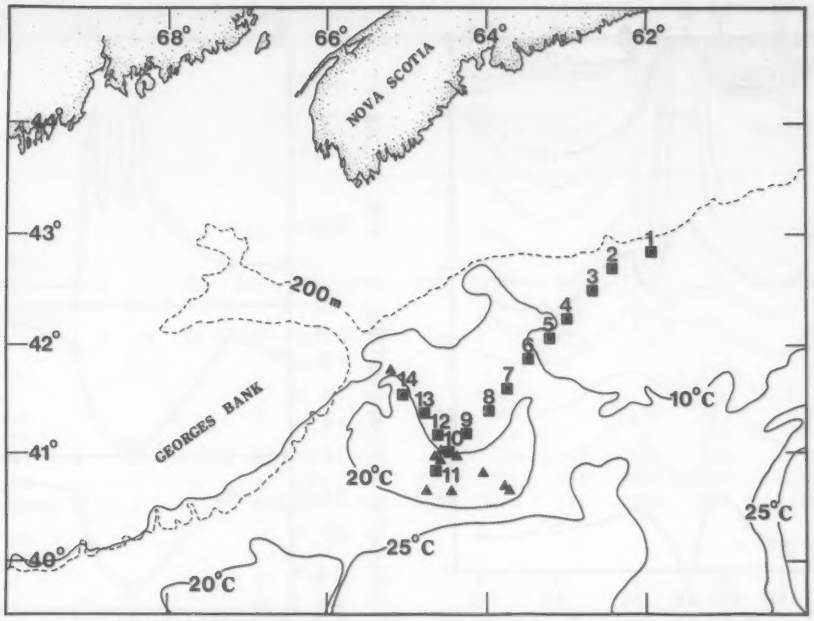


FIG. 3. Station locations for XBT drops (▲) and XBT drops with neuston and bongo net tows (■). The 10°C isotherm denotes the seaward extent of shelf water, the 20°C isotherm delimits surface features of the ring, and the 25°C isotherm indicates the shoreward extent of the Gulf Stream.

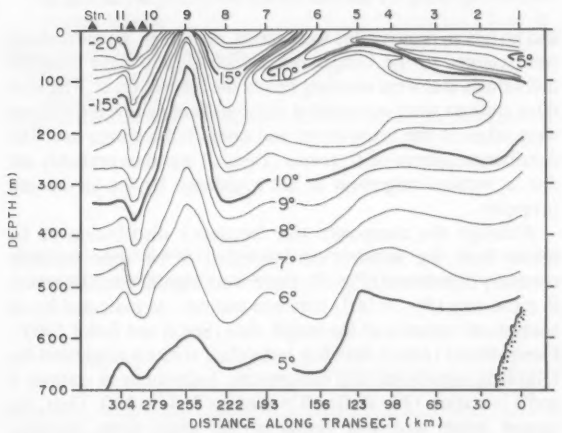


FIG. 4. Temperature section from XBT profiles along the transect into 81-G from the northeast (see Fig. 3).

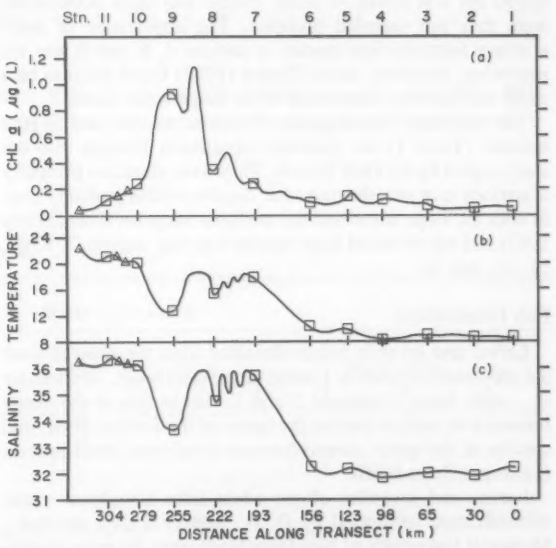


FIG. 5. Surface chlorophyll *a*, temperature, and salinity measured continuously along the transect from the northeast (see Fig. 3).

species in the study region, was found most abundantly at the first five stations and also at station 12 (Table 1). These abundances were low relative to the numbers usually found in more nearshore regions (Huntsman 1919; Sameoto 1973).

Eukrohnia hamata is a slope water mesopelagic species, although its juveniles can often be found within the upper 100 m of the water column (Cheney 1982). This species was found at the first seven stations and also at stations 9 and 12 but was absent from the ring interior stations (Table 1). *Sagitta tasmanica*, a slope water epipelagic species, was collected at all of the stations but was most abundant at the offshore sampling sites beyond station 3 (Table 1).

The five northern Sargasso Sea epipelagic species (Table 1) were abundant primarily at stations 7, 8, 10, 11, 13, and 14, which were in or near the ring. Abundances of the four northern Sargasso Sea mesopelagic species showed no consistent trends with hydrography. Their abundances were low relative to those of the epipelagic species. This was to be expected, since their populations live primarily below the 100-m depth to which the

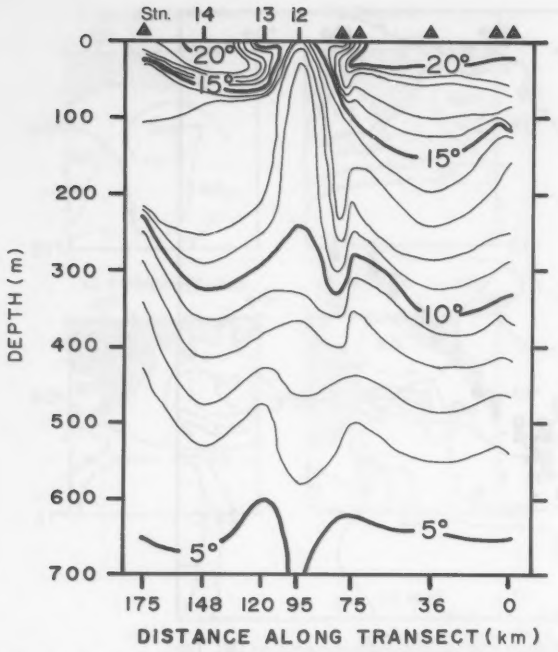


FIG. 6. Temperature section from XBT profiles along the transect out of 81-G toward the northwest (see Fig. 3).

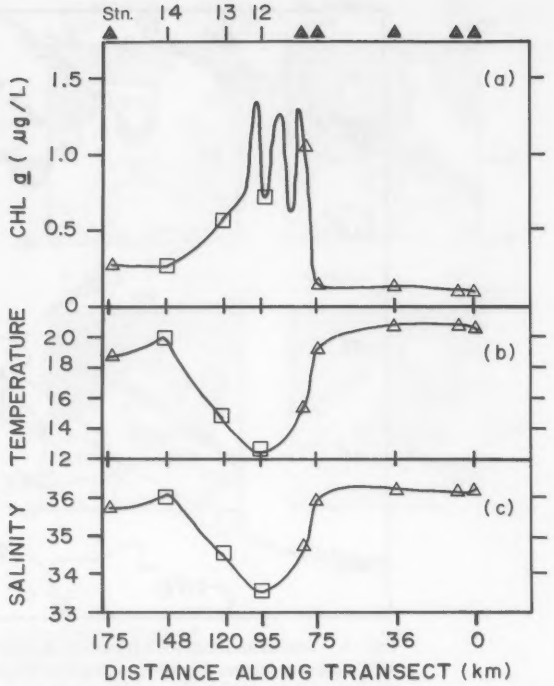


FIG. 7. Surface chlorophyll *a*, temperature, and salinity measured continuously along the transect toward the northwest (see Fig. 3).

bongo net was towed (Cheney 1982), and these populations were thus not sampled properly. The appearance of these northern Sargasso Sea species at stations 4, 5, and 6 was not surprising, however, since Cheney (1982) found them to be a small but constant component of the slope water fauna.

The epipelagic chaetognaths *Krohnitta pacifica* and *Sagitta helenae* (Table 1) are probably expatriates brought into the study region by the Gulf Stream. They were abundant primarily at stations in or near the ring core. *Sagitta enflata* probably lives in both the slope water and the northern Sargasso Sea (Cheney 1982) and we observed large numbers at ring stations 7, 8, 10, 11, 13, and 14.

Fish Distributions

Larval and juvenile fishes identified from the neuston tows are presented in Table 2. Larvae of the sand lance, *Ammodytes* sp., were found at stations 2 and 3. Adults live in the sandy bottom both inshore and on the banks of the Scotian Shelf, and species of the genus *Ammodytes* are considered shelf species (Leim and Scott 1966).

Larvae and juveniles of the white hake *Urophycis tenuis* (identification confirmed by D. A. Methven, Dep. of Biol., Memorial University of Newfoundland) were the most numerous of all fish species caught in the neuston tows. *Urophycis tenuis* occurred primarily in slope water (station 9) and in regions of the ring that were mixing with slope water (stations 7 and 8 in Table 2). *Urophycis tenuis* spawn on the Scotian Shelf and near the continental shelf break (Markle et al. 1982), so their larvae can be expected to be found in both shelf and slope water.

Markle et al. (1982) reported that the catchability of neustonic juveniles was somewhat greater at night. The first three tows along the transect were conducted in the afternoon and no larvae or juveniles were taken. However, no individuals were caught in the bongo net, which should have sampled individuals that were residing below the surface layer. The next three stations were occupied at night and only a few individuals were taken in the neuston net and none in the bongo net. The distribution pattern of *U. tenuis* (Table 2) was thus probably not due to vertical migration or net avoidance by the larvae and juveniles.

Although the composite size frequency distribution of *U. tenuis* from the neuston net appeared to be approximately normally distributed (Fig. 8), there were significant differences in mean size ($P < 0.001$) between stations, as indicated by an analysis of variance of the length data (Sokal and Rohlf 1969). Comparisons (*t*-test) between individual stations suggested the following significant size differences: individuals at stations 4 and 5 > station 12 > station 9 > stations 7, 8, and 10. Thus, the largest mean size was found at the shelf–slope stations, intermediate mean sizes were found at the slope water stations, and the smallest mean sizes were found at the ring stations.

Several species with reproducing slope water and/or northern Sargasso Sea populations were also collected in the neuston net (Table 2). *Ceratoscopelus maderensis* is a myctophid that lives in slope water and in the northern Sargasso Sea (Backus et al. 1977). *Centrobranchus nigrooscellatus* and *Gonichthys coccoi* are tropical and subtropical myctophids that are commonly found in the northern Sargasso Sea (Backus et al. 1977). *Histrio histrio*, the Sargassum fish, is commonly found in association with the Sargassum weed (Leim and Scott 1966). We should note that Sargassum weed was collected in neuston tows at all ichthyoplankton sampling stations.

Those species from the neuston tows that could not be identified as having reproducing populations on the Scotian

TABLE 1. Chaetognath abundance (No./1000 m^3) from bongo net tows.

	Water origin/station													
	Shelf			Shelf–slope			Ring		Slope	Ring		Shelf–slope	Ring	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Shelf species														
Sagitta elegans	1	5		11	4							5		
Slope species (epipelagic)														
Sagitta tasmanica	14	15	23	510	747	1776	2380	2386	696	1249	75	858	2543	1366
Slope species (mesopelagic)														
Eukrohnia hamata	8	18	39	36	77	39	44		125			77		
Northern Sargasso Sea species (epipelagic)														
Pterosagitta draco				2			176	169		216	791	5	156	195
Sagitta bipunctata							22	48			75			49
Sagitta hexaptera				10	8		88	48	42	144	188	9	196	
Sagitta minima				2	138	16	2072	771	104	2619	14419	18	7785	3415
Sagitta serratodentata				51	165	39	3183	2000	135	4108	3953	59	6220	8488
Northern Sargasso Sea species (mesopelagic)														
Krohnitta subtilis				2	4	8					38			
Sagitta decipiens				2										
Sagitta lyra	1			19	42	8	22	48	31		75	5	39	
Sagitta planctonis				2	4	16								
Gulf Stream–expatriate species (epipelagic)														
Krohnitta pacifica							66	120		168	339		39	49
Sagitta helenae						8	926	482	21	72	113	5	313	732
Slope water–Northern Sargasso Sea species (epipelagic)														
Sagitta enflata					8		6501	2048	62	2979	4329	5	2308	6634

TABLE 2. Larval and juvenile fish abundance (No./h) from neuston net tows.

	Water origin/station													
	Shelf			Shelf–slope			Ring		Slope	Ring		Shelf–slope	Ring	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Shelf species														
Ammodytes sp.		2	2											
Shelf–slope species														
Urophycis tenuis				3	2	7	146	209	60	17	2	9	5	2
Slope species														
Ceratoscopelus maderensis								5					14	2
Sargasso Sea species														
Centrobranchus nigroocellatus				2										
Gonichthys coccoi							3							
Histrio histrio				2							2			
Migrant–expatriate species														
Mugil curema							3	7						
Pomatomus saltatrix									2					
Scomberesox saurus						1	2				4			4

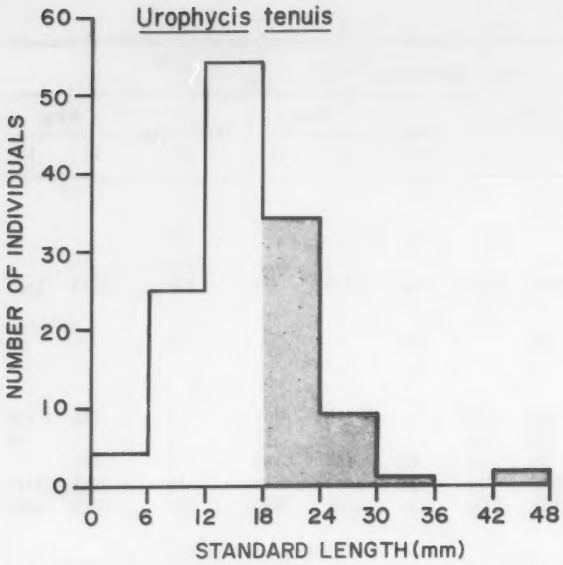


FIG. 8. Length–frequency histogram of neustonic *U. tenuis* from all stations. The unshaded portion designates larvae and the shaded portion represents juveniles, defined as individuals >18 mm standard length.

Shelf, in the slope water, or in the northern Sargasso Sea were classified as migrant–expatriate species (Table 2). Adults of the shelf species *Mugil curema* (white mullet) and *Pomatomus saltatrix* (bluefish) rarely occur north of Cape Cod (Breder 1948; Leim and Scott 1966). *Scomberesox saurus* (Atlantic saury) is a warm water coastal and oceanic species (Leim and Scott 1966).

A shelf–slope species not present in the neuston tows but found in the bongo samples was *Citharichthys arctifrons* (Gulf Stream flounder) (Table 3). Markle et al. (1980) suggested that this species has a breeding population on the continental shelf and slope off Nova Scotia. Also caught in the bongo net were larvae of *Sebastes* sp. The species is either the shelf redfish *S. fasciatus* or the deepwater redfish *S. mentella*, both of which occur near the edge of the Scotian Shelf where the sample was taken (Ni 1982).

Of the 10 species of slope water fishes found in the bongo net samples (Table 3), 6 were myctophids: *Benthosema glaciale*, *Ceratoscopelus maderensis*, *Diaphus* sp., *Hygophum benoiti*, *Myctophum punctatum*, and *Symbolophorus veranyi* (Backus et al. 1977). Haedrich (1972) reported *B. glaciale* and *C. maderensis* from a midwater trawl in a warm core ring located south of Georges Bank. The next three genera, *Cyclothone*, *Notolepis*, and *Stomias*, have common mesopelagic representatives in the slope water, and *Vinciguerria attenuata* is also a common slope water mesopelagic species (Leim and Scott 1966; Rofen 1966; Grey 1964). Sargasso Sea species caught in the bongo net samples at ring stations include the myctophid *Diogenichthys atlanticus* (Backus et al. 1977) and the mesopelagic fish *Omosudis lowei* (Rofen 1966).

In Table 3 we have called migrant–expatriate species those fishes that inhabit waters south of the Scotian Shelf but that again could not be clearly identified as having reproducing slope water or northern Sargasso Sea populations. These include the tropical serranid *Anthias* sp., the flounders *Bothus ocellatus* and *Etropus microstomus*, the blackbelly rose fish *Helicolenus dactylopterus*, the tongue fish *Symphurus* sp., and the snakefish *Trachinocephalus myops* (Hildebrand and Schroeder 1927; Anderson et al. 1966; Leim and Scott 1966). Adult specimens of *H. dactylopterus* have been found in slope water off Nova Scotia and might possibly be spawning there (D. Markle, Huntsman Marine Laboratory, St. Andrews, N.B., pers. comm.).

Also included in this category of migrant–expatriate species are two subtropical mesopelagic fishes, *Diplospinus multistriatus* and *Gempylus serpens* (Parin 1968). We caught one leptocephalus larva of *Facciollela* sp., a nettastomatid eel, which are found primarily in tropical waters (Smith and Castle 1982), and one specimen of *Caulophryne* sp., a bathypelagic fish with a poorly known distribution (Pietsch 1979).

Discussion

The abundances of those chaetognath species used as water mass indicators suggest the following types of water at the station locations. Stations 1, 2, and 3 were in primarily shelf water with perhaps a small slope water component indicated by the presence of small numbers of *E. hamata* and *S. tasmanica*. Stations 4, 5, 6, and 12 were probably a mixture of shelf and slope water as indicated by the increased abundances of the slope water species *E. hamata* and *S. tasmanica*. There may have been a small component of Gulf Stream and/or northern Sargasso Sea water as indicated by the presence of many of the northern Sargasso Sea species in small numbers. Their presence was to be expected, since the upper 150–200 m of the slope water is by nature a mixture of shelf water and Gulf Stream–northern Sargasso Sea water (McLellan 1956; Lee 1970).

Station 9 was in a water mass primarily of slope water origin as indicated by the relatively low abundances of the northern Sargasso Sea epipelagic and Gulf Stream expatriated species and by the presence of the slope water species *E. hamata*. The epipelagic chaetognath *S. enflata* is typically abundant in both the slope water and northern Sargasso Sea. Its relative absence from the slope water stations is difficult to interpret without further knowledge of its biology.

Stations 7, 8, 10, 11, 13, and 14 produced large numbers of northern Sargasso Sea epipelagic and Gulf Stream expatriated species and thus indicate the water to be a warm core ring with northern Sargasso Sea-Gulf Stream origin. The absence of the mesopelagic slope water species *E. hamata* from all these stations except station 7 also supports this conclusion.

The presence of the epipelagic slope water species *S. tasmanica* at the ring stations indicates that some mixing with slope water has occurred. But mixing and/or advection from the surrounding slope water alone cannot explain the large abundances of *S. tasmanica* observed in the ring, because the ring abundances were larger than those found at the slope water station 9. The most likely hypothesis to explain these patterns is that mixing process introduced *S. tasmanica* into the ring and a subsequent population expansion (i.e. birth rates greatly exceeded death rates) led to the large abundances found in the ring. The observed population increase is well within the reproductive capability of chaetognaths (Reeve 1970). In a similar instance, a large population of *S. tasmanica* has been observed in warm core ring 82-B (J. Cheney, unpubl. data). Other zooplankton and midwater fish species have been

TABLE 3. Larval and juvenile fish abundance (No./1000 m^3) from bongo net tows.

	Water origin/station												
	Shelf			Shelf–slope			Ring		Slope	Ring		Shelf–slope	Ring	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Shelf–slope species														
Citharichthys arctifrons										6				2
Sebastes sp.				10										
Urophycis tenuis							69	3					2	
Slope species														
Benthosema glaciale		1		34		18	124	18			85	27	7	151
Ceratoscopelus maderensis							176	84		105	5		7	6
Cyclothone sp.														246
Diaphus sp.		1		2			6							2
Hygophum benoiti													2	
Myctophum punctatum											5			
Notolepis sp.				2		2	3			3		2		
Stomias sp.						2				3				
Symbolophorus veranyi							3							
Vinciguerria attenuata							6							
Sargasso Sea species														
Diogenichthys atlanticus										9				2
Omosudis lowei							22							
Migrant–expatriate species														
Anthias sp.														2
Bothus ocellatus										3				3
Caulophryne sp.														2
Diplospinus multistriatus											7			5
Etropus microstomus											2			2
Facciollela sp.												2		
Gempylus serpens							3							
Helicolenus dactylopterus							3							
Symphurus sp.											2			
Trachinocephalus myops														3

observed in cold core rings in greatly increased abundances relative to their numbers in the northern Sargasso Sea and slope water (The Ring Group 1981).

In summary, the chaetognath data support indications from the temperature and salinity data that stations 1, 2, and 3 were in shelf water, stations 4, 5, 6, and 12 were in a mixture of shelf and slope water, station 9 was in primarily slope water, and stations 7, 8, 10, 11, 13, and 14 sampled a warm core ring with water of northern Sargasso Sea–Gulf Stream origin.

Because the major purpose of the cruise was to search for evidence of ring-induced, offshore advection of larvae of fish species from the Scotian Shelf, the shelf and shelf–slope fishes caught in the neuston and bongo net tows are of particular interest. Finding several sand lance (*Ammodytes* sp.) larvae in shelf water near the continental shelf break was to be expected. However, the large numbers of larval and juvenile *U. tenuis* that we found in slope water and regions of the ring that were mixing with slope water were not anticipated. Curiously, we did not find larvae of other common shelf fishes that spawn at this time, such as cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) (O'Boyle et al. 1984). Evseenko (1982) conducted an ichthyoplankton survey from the edge of the Scotian Shelf to the Gulf Stream in late autumn 1974 and found no larvae of fishes inhabiting the shelf. However, no warm core rings were present in the sampling area at the time (Noskov et al. 1977).

Markle et al. (1982) reported that in summer, adult *U. tenuis* are found on the Scotian Shelf and continental slope down to depths of at least 400 m. They suggested that spawning occurs year round, possibly with a peak of spawning activity in winter. Musick (1969) also concluded that *U. tenuis* on the southern Scotian Shelf spawn aperiodically, presumably with poor success relative to the more regular summertime spawning of stocks in the Gulf of St. Lawrence. It is likely that the larvae and juveniles we observed were spawned on the Scotian Shelf or upper continental slope.

The fact that individuals were on average smaller at the ring stations than at the shelf–slope water stations may indicate that the conditions for growth offshore were less than optimal. Markle et al. (1982) estimated that *U. tenuis* larvae grow at about 10–22 mm/mo. If we use the minimum growth rate of 10 mm/mo, then the individuals found at the ring stations may be between 1 and 2 mo old. This would place their birth date sometime in April or May when WCR 81-G was actively entraining shelf water off the Scotian Shelf (see Fig. 2).

Juvenile *U. tenuis* become demersal upon reaching sizes of 50–60 mm total length (Markle et al. 1982). Since the nursery grounds for the youngest demersal juveniles are shallow inshore waters and estuaries (Musick 1969), the fate of the larvae and juveniles we observed at the slope water and ring stations is uncertain. Losses by ring-induced offshore advection may

explain the poor recruitment rate of southern Scotian Shelf and New England stocks of *U. tenuis* relative to Gulf of St. Lawrence and Bay of Fundy stocks referred to by Musick (1969) and Markle et al. (1982). Several events in late winter and spring 1982 where shelf water extended all the way offshore to the Gulf Stream are depicted in Fig. 2d, 2f, 2g, and 2h. The dynamical role of warm core rings in mediating these events has been discussed by Louis and Smith (1982). Larval and juvenile fishes caught in these offshore flows are probably lost from their source populations.

A second purpose of the cruise was to determine whether warm core rings are a source of the tropical–subtropical larval fish species recorded by Markle et al. (1980) from ichthyoplankton surveys on the Scotian Shelf. The ichthyoplankton associated with the ring included several species that were reported by Markle et al. (1980) as expatriated larvae. These are *Anthias* sp., *B. ocellatus*, *G. coccoi*, *Symphurus* sp., and *T. myops*. We also found *C. arctifrons* larvae both in the ring and in shelf–slope water samples. Markle et al. (1980) regarded this species as having a reproducing population on the Scotian Shelf. Perhaps warm core rings are a continual source of larvae of this species from more southern populations.

It is quite apparent from satellite imagery of sea surface temperature that rings can advect complex mixtures of slope water and Gulf Stream water onto the continental shelf. The frontal analysis chart for 28 June 1982 (Fig. 2l) clearly shows slope water overriding the southern edge of Georges Bank with WCR 81-G entraining shelf water behind it. WCR 81-G did not approach the Scotian Shelf closely enough to cause a similar exchange of water (Fig. 1) but it certainly had the potential (Halliwell and Mooers 1979). It is therefore easy to understand how planktonic larvae associated with the Gulf Stream and northern Sargasso Sea can be occasionally transported onto the continental shelf.

Acknowledgments

A number of people contributed to this research. Bruce Burns of the U.S. National Marine Fisheries Service identified the larval and juvenile fishes. David Methven of the Department of Biology, Memorial University of Newfoundland, aided in differentiating *U. tenuis* from *U. chuss*. Peter Celone and J. Lockwood Chamberlin of the U.S. National Marine Fisheries Service, Atlantic Environmental Group, supplied the trackline of WCR 81-G and oceanographic frontal analysis charts. Robert Fournier of the Department of Oceanography, Dalhousie University, provided the surface temperature, salinity, and chlorophyll data. The Warm Core Rings Program of the National Science Foundation supplied the XBTs. We thank G. Laurence, D. Methven, J. Craddock, and D. Markle for valuable comments on the manuscript. We also thank the officers and crew of the C.S.S. *Dawson*. This research was supported by grants from the Natural Sciences and Engineering Research Council of Canada and the National Science Foundation.

References

ANDERSON, W. M., J. W. GEHRINGER, AND F. H. BERRY. 1966. Family Synodontidae, p. 30–102. *In* G. W. Mead [ed.] Fishes of the western North Atlantic. Sears Foundation for Marine Research Memoir 1, Part 5.

BACKUS, R. H., J. E. CRADDOCK, R. L. HAEDRICH, AND B. H. ROBISON. 1977. Atlantic mesopelagic zoogeography, p. 266–287. *In* D. M. Cohen [ed.] Fishes of the western North Atlantic. Sears Foundation for Marine Research Memoir 1, Part 7.

BREDER, C. M. 1948. Field book of marine fishes of the Atlantic coast. G. P. Putnam's Sons, New York, NY. 332 p.

CHENEY, J. 1982. The spatial and temporal abundance patterns of chaetognaths in the western North Atlantic Ocean. Ph.D. thesis, Massachusetts Institute of Technology/Woods Hole Oceanographic Institution, Woods Hole, MA. 337 p.

EVSEENKO, S. A. 1982. Ichthyoplankton of slope and Gulf Stream waters off Nova Scotia in late autumn 1974. J. Northw. Atl. Fish. Sci. 3: 127–139.

FITZGERALD, J. L., AND J. L. CHAMBERLIN. 1982. Anticyclonic warm core Gulf Stream rings off the northeastern United States during 1981. NAFO SCR Doc. 82/VI/10: 12 p. (Available from Northwest Atlantic Fisheries Organization, P.O. Box 638, Dartmouth, N.S. B2Y 3Y9)

FOURNIER, R. O., M. VAN DET, N. B. HARGREAVES, J. S. WILSON, T. A. CLAIR AND R. ERNST. 1984. Physical factors controlling summer distribution of chlorophyll *a* off southwestern Nova Scotia. Limnol. Oceanogr. (In press)

FRIEDLANDER, A., AND D. SMITH. 1983. Sand lance larvae found in entrainment feature associated with warm core ring off Hudson Canyon. Coastal Oceanogr. Climatol. News 5: 13–14. (Available from Center for Ocean Management Studies, University of Rhode Island, Kingston, RI 02881)

FUGLISTER, F. C. 1963. Gulf Stream '60. Prog. Oceanogr. 1: 265–283.

GREY, M. 1964. Family Gonostomatidae, p. 290–316. *In* H. B. Bigelow [ed.] Fishes of the western North Atlantic. Sears Foundation for Marine Research Memoir 1, Part 4.

HAEDRICH, R. L. 1972. Midwater fishes from a warm-core eddy. Deep-Sea Res. 19: 903–906.

HALLIWELL, G. R. JR., AND C. N. K. MOOERS. 1979. The space-time structure and variability of the shelf water-slope water and Gulf Stream surface temperature fronts and associated warm core eddies. J. Geophys. Res. 84: 7707–7725.

HILDEBRAND, S. F., AND W. C. SCHROEDER. 1927. Fishes of Chesapeake Bay. Dep. Commer. Bull. U.S. Bur. Fish. 43(1): 1–388.

HUNTSMAN, A. G. 1919. A special study of the Canadian chaetognaths, their distribution, etc. in the waters of the eastern coast. Rep. Dep. Nav. Serv. Can. Can. Fish. Exped. 1914–15: 421–485.

LEE, A. H. 1970. The T–S structure, circulation and mixing in the slope water region east of the Scotian Shelf. Ph.D. thesis, Dalhousie University, Halifax, N.S. 191 p.

LEIM, A. M., AND W. B. SCOTT. 1966. Fishes of the Atlantic coast of Canada. Fish. Res. Board Can. Bull. 155: 485 p.

LOUIS, J. P., AND P. C. SMITH. 1982. The development of the barotropic radiation field of an eddy over a slope. J. Phys. Oceanogr. 12: 56–73.

MARKLE, D. F., D. A. METHVEN, AND L. J. COATES-MARKLE. 1982. Aspects of spatial and temporal cooccurrence in the life history stages of the sibling hakes, *Urophycis chuss* (Walbaum 1792) and *Urophycis tenuis* (Mitchill 1815) (Pisces:Gadidae). Can. J. Zool. 60: 2057–2078.

MARKLE, D. F., W. B. SCOTT, AND A. C. KOHLER. 1980. New and rare records of Canadian fishes and the influence of hydrography on resident and nonresident Scotian Shelf ichthyofauna. Can. J. Fish. Aquat. Sci. 37: 49–65.

MAURER, R., D. BUSCH, AND J. GREEN. 1979. Observations on the slope/shelf front in the immediate vicinity of a warm eddy. Coastal Oceanogr. Climatol. News 2: 3–4. (Available from Center for Ocean Management Studies, University of Rhode Island, Kingston, RI 02881)

MCLELLAN, H. J. 1956. On the distinctness and origin of the slope water off the Scotian Shelf and its easterly flow south of the Grand Banks. J. Fish. Res. Board Can. 14: 213–239.

MUSICK, J. A. 1969. The comparative biology of two American Atlantic hakes, *Urophycis chuss* and *U. tenuis* (Pisces:Gadidae). Ph.D. thesis, Harvard University, Cambridge, MA. 150 p.

NI, I. H. 1982. Meristic variation in beaked redfishes, *Sebastes mentella* and *S. fasciatus*, in the Northwest Atlantic. Can. J. Fish. Aquat. Sci. 39: 1664–1685.

NOSKOV, A. S., A. M. PANKRATOV, I. K. SIGAEV, AND A. I. SHERSTYUKOV. 1977. Ecological survey in the Gulf Stream zone southward of Nova Scotia. Int. Comm. Northw. Atl. Fish. Res. Doc., No. 39, Ser. No. 5064: 7 p.

O'BOYLE, R. N., M. SINCLAIR, R. J. CONOVER, K. H. MANN, AND A. C. KOHLER. 1984. Temporal and spatial distribution of ichthyoplankton communities of the Scotian Shelf in relation to biological, hydrological and physiographic features. Rapp. P.-V. Reun. Cons. Int. Explor. Mer (In press).

PARIN, N. W. 1968. The ichthyofauna of the oceanic epipelagial. Nauka, Moscow. 186 p.

PIETSCH, T. W. 1979. Systematics and distribution of ceratioid anglerfishes of the family Caulophrynidae with the description of a new genus and species

from the Banda Sea, Indonesia. Nat. Hist. Mus. Los Ang. Cty. Contrib. Sci. 0(310): 1–25.

REEVE, M. R. 1970. The biology of the Chaetognatha. I. Quantitative aspects of growth and egg production in *Sagitta hispida*, p. 168–189. *In* J. H. Steele [ed.] Marine food chains. Oliver & Boyd Ltd., Edinburgh, Scotland.

ROFEN, R. R. 1966. Family Omosudidae, p. 462–481. *In* G. W. Mead [ed.] Fishes of the western North Atlantic. Sears Foundation for Marine Research Memoir 1, Part 5.

SAMEOTO, D. D. 1973. Annual life cycle and production of the chaetognath *Sagitta elegans* in Bedford Basin, Nova Scotia. J. Fish. Res. Board Can. 30: 333–344.

SMITH, D. G., AND P. H. J. CASTLE. 1982. Larvae of the nettastomatid eels: systematics and distribution. Dana-Rep. Carlsberg Found. 90: 1–44.

SOKAL, R. R., AND F. J. ROHLF. 1969. Biometry. W. H. Freeman and Co., San Francisco, CA. 776 p.

THE RING GROUP. 1981. Gulf Stream cold core rings: their physics, chemistry and biology. Science (Washington, DC). 212(4499): 1091–1100.

WORTHINGTON, L. V. 1976. On the North Atlantic circulation. The Johns Hopkins Oceanographic Studies No. 6. The Johns Hopkins University Press, Baltimore, MD. 110 p.

YODER, J. A., L. P. ATKINSON, T. N. LEE, H. H. KIM, AND C. R. MCCLAIN. 1981. Role of Gulf Stream frontal eddies in forming phytoplankton patches on the outer southeastern shelf. Limnol. Oceanogr. 26: 1103–1110.

Development of Larvae of the Saffron Cod, *Eleginus gracilis*, with Comments on the Identification of Gadid Larvae in Pacific and Arctic Waters Contiguous to Canada and Alaska

Jean R. Dunn and Beverly M. Vinter

Northwest and Alaska Fisheries Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 2725 Montlake Boulevard East, Seattle, WA 98112

Dunn, J. R., and B. M. Vinter. 1984. Development of larvae of the saffron cod, *Eliginus gracilis*, with comments on the identification of gadid larvae in Pacific and arctic waters contiguous to Canada and Alaska. Can. J. Fish. Aquat. Sci. 41: 304–318.

A developmental series (4.2–28.7 mm standard length, SL) of larvae and pelagic juveniles of the saffron cod, *Eleginus gracilis*, from the Bering and Chukchi seas is described and illustrated for the first time. Larvae of *E. gracilis* hatch at about 3.5 mm SL, and yolk is absorbed by about 6.5 mm SL. Notochord flexion commences at about 11 mm SL and is completed by about 17 mm; transformation to the pelagic juvenile stage occurs at about 24–27 mm SL. *Eleginus gracilis* larvae are characterized by gut pigment and by the presence of two distinctive postanal bars of pigment. They may be distinguished from other cooccurring gadid larvae in the Gulf of Alaska (walleye pollock, *Theragra chalcogramma*; Pacific cod, *Gadus macrocephalus*; Pacific tomcod, *Microgadus proximus*) as well as those in the Bering and Chukchi seas south of 70°N (*T. chalcogramma*, *G. macrocephalus*, and Arctic cod, *Boreogadus saida*) based on pigment patterns and meristic characters. Comments are included on the status of knowledge of larvae of three other gadids (in addition to *E. gracilis* and *B. saida*) present in North American arctic waters: ogac (*Gadus ogac*), toothed cod (*Arctogadus borisovi*) and polar cod (*A. glacialis*).

L'article qui suit décrit et illustre pour la première fois une série de phases de développement (4,2–28,7 mm de longueur standard, LS) de larves et de juvéniles pélagiques du navaga jaune, *Eleginus gracilis*, des mers de Béring et de Tchouktche. Les larves mesurent environ 3,5 mm LS à l'éclosion, et le vitellus est absorbé quand elles ont atteint 6,5 mm LS. La flexion de la notochorde commence à environ 11 mm LS et est terminée à environ 17 mm LS; la transformation en juvéniles pélagiques se produit à environ 24–27 mm LS. Les larves d'*E. gracilis* sont caractérisées par le pigment de l'intestin et par la présence de deux bandes postanales distinctives de pigments. Elles se distinguent des autres larves de gadidés qui se rencontrent également dans le golfe d'Alaska (morue du Pacifique occidental, *Theragra chalcogramma*; morue du Pacifique, *Gadus macrocephalus*; et poulamon du Pacifique, *Microgadus proximus*), ainsi que de celles des mers de Béring et de Tchouktche au sud de 70° de latitude N (*T. chalcogramma*, *G. macrocephalus* et le saïda, *Boreogadus saida*) par la disposition des pigments et certains caractères méristiques. L'article contient en plus des commentaires sur l'état de nos connaissances des larves de trois autres gadidés (en plus d'*E. gracilis* et *B. saida*) présents dans les eaux arctiques de l'Amérique du Nord : l'ogac (*Gadus ogac*), le saïda barbu (*Arctogadus borisovi*) et le saïda imberbe (*A. glacialis*).

Received February 23, 1983
Accepted November 1, 1983

Reçu le 23 février 1983
Accepté le 1 novembre 1983

Codfishes (Gadidae) occurring in pacific and arctic waters contiguous to Canada and Alaska are of considerable economic importance, and some of these species have long been the target of directed fisheries for sustenance or sale (Hart 1973; Morrow 1980). Until recently, however, certain size larvae of gadids occurring in waters of British Columbia and Alaska could not be specifically identified (Mattson and Wing 1978; Waldron 1981); this hindered the use of ichthyoplankton sampling as a technique in estimating year-class strength. Matarese et al. (1981) provided criteria for identification of larvae of three gadids, walleye pollock (*Theragra chalcogramma*), Pacific tomcod (*Microgadus proximus*), and Pacific cod (*Gadus macrocephalus*) in samples from the Northeast Pacific Ocean in which they might cooccur.

Presented here is the first complete description of the development of the saffron cod, *Eleginus gracilis*. We also provide criteria and comparative illustrations that should now enable specific identification in mixed samples of larvae of *E. gracilis*, *T. chalcogramma*, *G. macrocephalus*, *M. proximus*, and the Arctic cod, *Boreogadus saida*. We further discuss the status of knowledge of larvae of gadids occurring in arctic waters of Canada and Alaska.

Eleginus gracilis ranges from about Sitka, Alaska, through the Bering and Chukchi seas, eastward to Cambridge Bay in the Beaufort Sea, and westward to the Sea of Japan and Okhotsk

TABLE 1. Collection locations of larvae of *Eleginus gracilis*.

Vessel	Station	Date	Latitude (N)	Longitude (W)	Gear[a]	Mesh (mm)	Depth of tow (m)	Bottom depth (m)	No. of Larvae	Length range (mm SL)
—	23	July 7, 1977	64°10.10′	164°07.06′	STN	1.6	—	—	2	12.7, 14.8
	42	July 10, 1977	64°30.20′	163°20.35′	STN	1.6	—	—	4	17.5–28.7
Hakuho Maru	22	July 24, 1978	69°09.8′	168°37.2′	ORI	1.0	35	—	1	10.1
Polar Star	4	May 6, 1980	60°27.0′	178°16.4′	PLM	0.571	162	164	1	5.5
	10	May 9, 1980	60°04.40′	176°54.27′	B	0.505	137	137	1	4.9
	13	May 11, 1980	60°15.20′	173°45.24′	B	0.505	71	83	1	6.1
	16	May 12, 1980	60°13.53′	175°29.56′	B	0.505	115	115	1	9.4
	19	May 14, 1980	61°29.6′	174°44.1′	B	0.505	69	84	3	6.3–12.2
	20	May 14, 1980	61°43.42′	175°32.00′	B	0.505	91	91	1	11.7
	21	May 14, 1980	61°31.12′	176°15′	B	0.505	92	102	1	12.5
	24	May 16, 1980	61°54.4′	177°4.5′	B	0.505	117	117	1	13.6
	26	May 22, 1980	62°10.3′	168°59.1′	B	0.505	32	38	1	14.7
	28	May 23, 1980	61°17.77′	169°50.59′	B	0.505	40	44	1	15.1
	29	May 24, 1980	61°47.5′	168°09.5′	B	0.505	26	28	1	16.2
	30	May 24, 1980	61°44.09′	167°07.5′	B	0.505	27	27	1	4.9
	47	June 7, 1980	65°59.87′	168°17.92′	PLM	0.571	53	55	12	4.2–26.6
	53	June 13, 1980	66°30.8′	167°22′	R	0.308	18	—	2	4.7, 6.1
	54	June 15, 1980	66°45.8′	168°33′	B	0.505	36	38	1	5.6
	57	June 16, 1980	65°06.3′	168°36.7	B	0.505	45	48	1	6.8
	58	June 17, 1980	64°48′	169°14′	B	0.505	50	50	2	4.8, 7.0

[a]STN, surface tow net; ORI, Ocean Research Institute (University of Tokyo) net; PLM, plummet net; B, 60-cm bongo net; R, 0.75-m ring net.

Sea (Walters 1955; Quast and Hall 1972; McAllister 1984). It is generally found in shallow depths over muddy bottoms, often in brackish waters; the species apparently reaches 35 cm in length and longevity is 6–7 yr (Svetovidov 1948; Morrow 1980). Little is known about their reproduction or early life history. Kozlov (1952) and Mukhacheva (1957) described the demersal, nonadhesive eggs of *E. gracilis*, and Mukhacheva (1957) illustrated artificially reared larvae 3.8–5.2 mm standard length (SL), which hatched in 36 d at a mean temperature of 2.2°C (range −2.0 to +8.0°C). Larger specimens, however, have not been described.

Saffron cod larvae are relatively rare in plankton collected in the Northeast Pacific Ocean. They have not been reported in plankton collected in inland coastal waters of southeastern Alaska (Mattson and Wing 1978) nor were they taken in extensive plankton sampling in the Kodiak Island region (Kendall et al. 1980) or near the Alaska Peninsula (Bates and Clark 1983). They were infrequently reported in limited plankton sampling in the northern Bering Sea and the Chukchi Sea (Waldron 1981); in contrast, they were the third most abundant larvae collected in Tuktoyaktuk Harbor, Northwest Territories, in mid-July to mid-August 1982 (Ratynski 1983).

At certain sizes, larvae of *E. gracilis* can be confused with cooccurring gadid larvae. In the Gulf of Alaska, these include *T. chalcogramma*, *G. macrocephalus*, and *M. proximus*. In the Bering and Chukchi seas (south of 70°N), cooccurring gadids include *E. gracilis*, *G. macrocephalus*, and *B. saida* (Quast and Hall 1972; Wolotira et al. 1977). Gadids reported from arctic waters contiguous to Canada and Alaska are *E. gracilis*, *B. saida*, the ogac (*Gadus ogac*), polar cod (*Arctogadus glacialis*), and toothed cod, *Arctogadus borisovi* (Boulva 1972; McAllister 1984).

Larvae of *B. saida* were described by Schmidt (1905) and Russell (1976), *T. chalcogramma* by Gorbunova (1954) and Yusa (1954), *G. morhua macrocephalus* by Gorbunova (1954), Uchida et al. (1958), and Mukhacheva and Zviagina (1960), and *M. proximus* by Matarese et al. (1981). Larvae of *A. borisovi* were partially described by Zviagina (1961), but neither *A. glacialis* nor *G. ogac* larvae have been described.

Materials and Methods

Specimens

A developmental series of 39 larvae and early juveniles (4.2–28.7 mm SL) of *E. gracilis* was assembled from a variety of sources (Table 1). Demersal juvenile specimens were donated by the University of British Columbia. *Boreogadus saida* larvae and juveniles were also assembled from collections made in the Bering and Chukchi seas. Juvenile *B. saida* collected from the Chukchi Sea were loaned by the Auke Bay Laboratory, Northwest and Alaska Fisheries Center (NWAFC), Juneau, and by the Alaska Department of Fish and Game, Fairbanks. Comparative samples consisting of an extensive series of larvae and juveniles of *G. macrocephalus*, *T. chalcogramma*, and *M. proximus* were available from the archives of the NWAFC. All larval specimens used in this study are archived at the NWAFC.

Terminology

Terminology of developmental stages follows Ahlstrom et al. (1976). Methods of body measurements follow Matarese et al. (1981) except for caudal peduncle depth, which follows Laroche and Richardson (1981). All lengths used here are standard lengths (SL), i.e. from the tip of the snout to the end of the notochord prior to caudal fin development and then to the posterior margin of the superior hypural bone. Illustrations were made by the junior author with the aid of a camera lucida.

TABLE 2. Summary of counts of meristic structures in adult *Eleginus gracilis* and *Boreogadus saida* (Data from this study except as noted).

Species	Fin rays							Gill rakers			Vertebrae		
	First dorsal	Second dorsal	Third dorsal	First anal	Second anal	Pectoral	Pelvic	Superior hypural	Upper	Lower	Total	Precaudal	Caudal	Total
E. gracilis	11–16[a]	15–24	17–24	20–27[a]	18–23[a]	18–20	6	5	2–3	17–20	18–23	21–24	37–41	57–64[a]
B. saida	11–16	12–17[a]	17–23[a]	14–20[a]	18–24[a]	18–21	6	4	7–10	31–34	37–46[a]	18–19	36–39	53–58[a]

[a]From Svetovidov (1948).

Counts of meristic structures were made on cleared and stained larvae (Dingerkus and Uhler 1977). Additional counts of meristic structures were made from radiographs to determine ranges of counts, following Matarese et al. (1981). Stained samples were also used to determine the onset and sequence of ossification of bones. Variation can occur in the ability of bones to accept alizarin red stain (Dunn 1983), and structures were considered ossified even if only slightly stained. Terminology of bones follows Mujib (1967) and Harrington (1955), except for the caudal fin. Terminology of hypural bones follows Matarese et al. (1981), and designation of caudal fin rays follows Markle (1982).

Nomenclature

We follow Svetovidov (1948, 1965) and Morrow (1980) in considering the species of *Eliginus* resident in North American waters as *E. gracilis*. Walters (1955) indicated that the saffron cod of arctic America is meristically intermediate between *E. navaga* of Europe and Siberia, and he considered the North American form to be *E. navaga navaga*. Walters further suggested that the *Eleginus* of the southern Chukchi Sea may be *E. navaga gracilis*, the subspecies found in Siberia. Svetovidov (1965), however, considered the considerable differences in parapophyses shape and gill raker numbers (14–24 in *E. gracilis* and 23–28 in *E. navaga*) as convincing evidence of specific differences in the two nominal forms. The resolution of the correct name and the specific status of the nominal species of *Eleginus* is, however, beyond the scope of this paper.

Verification of Identification

A developmental series of *E. gracilis*, ranging from yolk-sac larvae to early pelagic juveniles, was linked together by pigment patterns, myomere counts, caudal fin development, and, in juvenile specimens, counts of other meristic structures. The series was identified as gadid based on several criteria: (1) morphology and pigmentation characteristic of gadid larvae (Russell 1976; Matarese et al. 1981), (2) in small larvae (<10 mm) the vent opens laterally through the fin-fold (Matarese et al. 1981), and (3) the development of a "pseudocaudal" fin (Ahlstrom and Counts 1955; Matarese et al. 1981) in which the procurrent caudal fin rays begin forming before the primary caudal fin rays. Considering the area of collection (northern Bering Sea and the Chukchi Sea, south of 70°N), the series could be one of only four species of gadids resident in the area (Quast and Hall 1972; Wolotira et al. 1977): *E. gracilis*, *B. saida*, *T. chalcogramma*, or *G. macrocephalus*.

Larvae of the congener of *E. gracilis*, *E. navaga*, have been partially described from samples collected in the Barents and White seas of northern Europe (Kusmin-Karawajew 1930; Khaldinova 1936; Rass 1949; Ponomareva 1949). Unfortunately, none of these papers provide sufficient detail to assist materially in the identification of *E. gracilis* larvae.

The relatively high myomere counts (57–64) and distribution of pigment eliminated both *T. chalcogramma* and *G. macrocephalus* from consideration in the identification of the series based on published criteria (Gorbunova 1954; Mukhacheva and Zviagina 1960; Matarese et al. 1981). Counts of meristic structures (particularly precaudal vertebrae, number of fin rays in the second dorsal fin and first anal fin, gill raker counts, and number of rays on the superior hypural bone) in juvenile

TABLE 3. Body proportions of larvae and juveniles of *Eleginus gracilis*. Values given for each body proportion are expressed as percentage of standard length (SL) or head length (HL): mean, standard deviation, and range (in parentheses).

Body proportion	Preflexion	Flexion	Postflexion	Transforming	Pelagic juvenile
Sample size	17[a]	12	2	3	1
Standard length (mm)	6.0±1.6 (5–10)	13.5±1.5 (11–16)	19.1±2.2 (18–21)	24.3±1.8 (23–26)	27.2 (27)
Snout to anus length/SL	42.1±5.4 (38–60)	49.4±1.9 (46–53)	47.7±3.6 (45–50)	45.8±2.2 (44–48)	47.1 (47)
Head length/SL	19.7±3.2 (16–29)	26.4±1.7 (23–29)	29.3±3.0 (27–31)	26.0±0.8 (25–27)	25.4 (25)
Eye diameter/HL	39.2±4.7 (30–47)	32.3±1.4 (30–35)	30.3±2.8 (28–32)	29.0±1.2 (28–30)	27.8 (28)
Snout length/HL	16.3±3.4 (13–26)	21.1±3.5 (15–27)	24.0±5.1 (20–28)	26.3±1.3 (25–28)	27.7 (28)
Upper jaw length/HL	47.6±10.3 (34–71)	36.3±6.1 (28–46)	41.4±1.4 (40–42)	39.1±2.7 (38–42)	38.6 (39)
Body depth at pectoral fin base/SL	15.0±2.5 (10–21)	20.9±1.5 (18–24)	20.6±2.4 (19–22)	19.9±0.3 (20)	20.6 (21)
Depth at anus/SL	7.6±2.8 (4–15)	15.1±1.6 (13–18)	17.6±0.2 (17–18)	18.2±0.1 (18)	19.9 (20)
Snout to first dorsal fin/SL	33.7 (34)	37.1±2.1 (32–40)	36.0±0.8 (35–37)	33.9±1.3 (33–35)	33.5 (34)
Snout to second dorsal fin/SL	43.6 (44)	48.5±2.0 (44–51)	46.9±2.4 (45–49)	45.6±0.9 (44–46)	44.1 (44)
Snout to third dorsal fin/SL	58.4 (58)	68.4±3.7 (62–75)	70.5±2.2 (69–72)	66.7±1.0 (66–67)	66.9 (67)
Snout to first anal fin/SL	48.5 (49)	50.4±2.0 (47–54)	49.1±4.1 (46–52)	46.6±2.1 (45–49)	47.8 (48)
Snout to second anal fin/SL	63.4 (63)	69.6±2.6 (66–76)	69.0±0.2 (69)	66.8±1.5 (66–68)	66.5 (67)
Caudal peduncle depth/SL	5.9 (6)	7.3±1.1 (6–10)	7.3±0.6 (7–8)	7.4±0.2 (7–8)	7.0 (7)

[a]Sample size for snout to anus length is 16; sample size for snout to dorsal fins, snout to anal fins, and caudal peduncle depth is 1.

specimens provided conclusive evidence that the series was *E. gracilis* as opposed to *B. saida* (Table 2).

Results

Morphology of *E. gracilis*

Larvae hatch at about 3.5 mm (Mukhacheva 1957). Yolk absorption is complete at about 6.5 mm. In 4.2-mm larvae, vent opens laterally on right side, becomes vertical in 10 mm larvae. Notochord flexes at about 11 mm, flexion completed by 16–17 mm, transformation occurs at 24–27 mm. Head length (as percentage of SL) increases from nearly 20% in preflexion larvae to approximately 26% in transforming and juvenile specimens (Table 3). Eye diameter declines (as percentage of head length) from approximately 39% in preflexion larvae to about 28% in pelagic juveniles. Snout length/head length increases from 16% in preflexion larvae to nearly 28% in pelagic juveniles. Distances from snout to each dorsal and anal fin remain relatively constant during development.

Larvae moderately slender, greatest body depth occurring at pectoral fin base. This depth increases from about 15% SL in preflexion larvae to about 20% SL in larger larvae and transforming juveniles (Table 3). Body tapers posteriorly. Depth at anus increases from about 8% SL in preflexion larvae to 18–20% SL in postflexion and larger specimens. Caudal peduncle depth relatively constant (about 7% SL). Snout–anus distance increases from 42% in preflexion larvae to 49% SL in flexion larvae.

Pigmentation

Although pigmentation is similar among gadid larvae in the Northeast Pacific Ocean and varies among larvae of *E. gracilis*, specific characters persist that aid in identification. We follow Matarese et al. (1981) in defining pigment "bars" in gadid larvae as anterior and posterior pigment areas on the trunk, each composed of a dorsal and ventral stripe.

Head pigmentation in small preflexion larvae (about 4.7–6.3 mm) consists principally of eye pigmentation and one to three internal (occasionally four) spots at base of brain in prootic–opisthotic region (Fig. 1A, 1B); the latter persist in various numbers until early juvenile stage. Zero to two pigment spots present on middle or posterior end of dentary; single melanophore may be present at tip of dentary. Single melanophore characteristically located at anterior to middle of cleithrum. In preflexion larvae (about 6.5–7.0 mm), one to five pigment spots appear in cluster on dorsal part of head, generally from mideye to posterior portion. Two to five single melanophores present ventrally on isthmus, and pigment on dentary increases to three to five melanophores. Internal spots in prootic-opisthotic region persist in various numbers (about 2–6) in preflexion larvae about 7–10 mm (Fig. 1C). Melanophores appear on head from tip of snout to posterior portion of head. Pigment develops on snout anterior to eye, posterior to dentary, on gular region and isthmus (Fig. 1C, 1D), and anterior to cleithrum. General trend of increased head pigmentation persists with growth through pelagic juvenile stage (about 24–27 mm). Pigment increases on gular region and on isthmus and develops posterior and anterior to eyes (Fig. 1E; 2A, 2B).

Preflexion larvae (about 5–10 mm) have pigment on gut region primarily associated with dorsal and ventral portions (Fig. 1A–1C). In smallest larvae (4.7 mm), oblique line of pigment present between dorsal margin of gut and ventral portion of body near vent; this line frequently extends continuously over dorsal margin of gut to tip of vent. Line of pigment present on ventral midline of gut, extending from cleithrum to midgut or to vent (Fig. 1D). In small larvae (about 5–7 mm), ventral gut pigment consists of about 8–25 spots in approximate double row with most pigment anterior. With growth of larvae (7–10 mm), ventral gut pigment increases (to about 16–38 melanophores, most on anterior two thirds of area), and pigment develops on dorsal body margin as continuation of postanal dorsal stripe (Fig. 1E). With further growth of larvae (Fig. 2A, 2B), gut pigment increases, with melanophores developing over lateral wall of gut. Ventral gut pigment persists even to pelagic juvenile stage (about 27 mm). One to several pigment spots

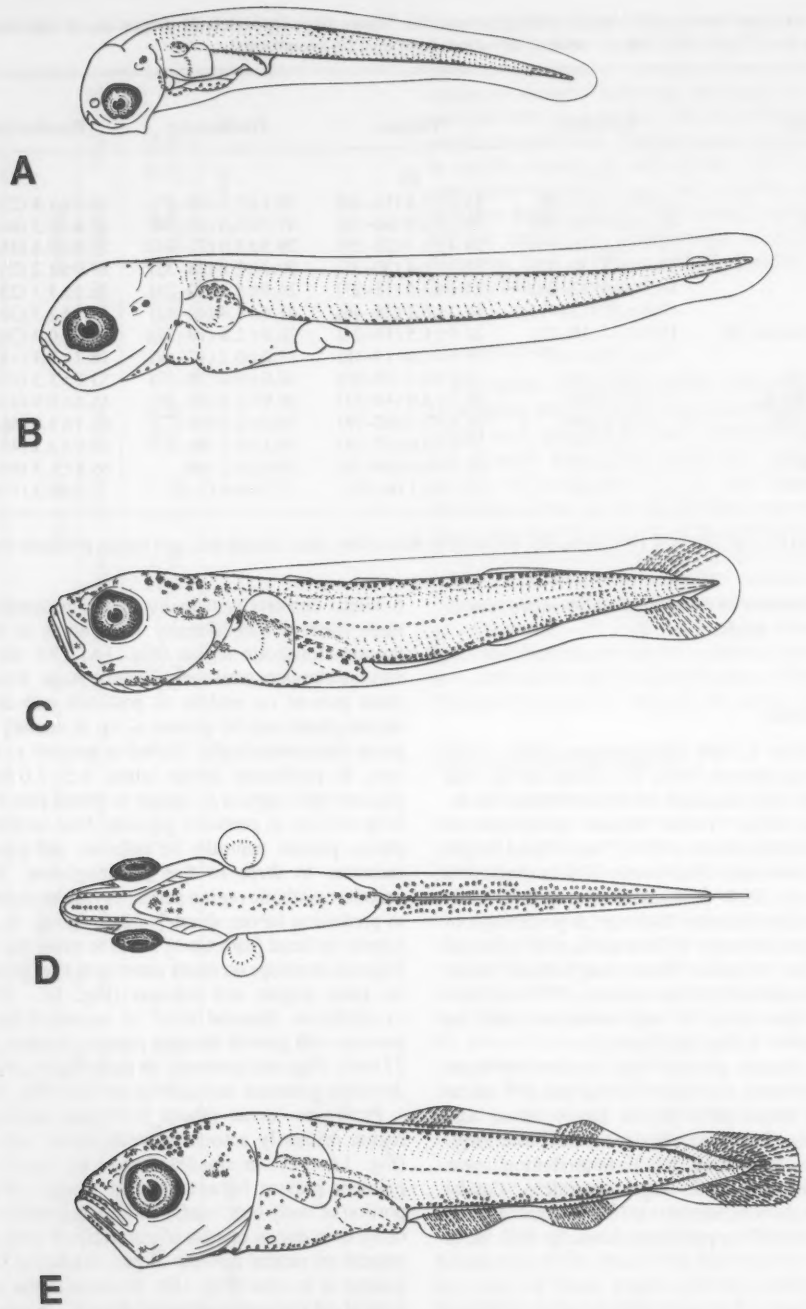


FIG. 1. Larval stages of *Elenius gracilis*. A, 5.0 mm SL; B, 7.0 mm SL; C, 10.1 mm SL; D, 10.1 mm SL (ventral view); E, 13.6 mm SL.

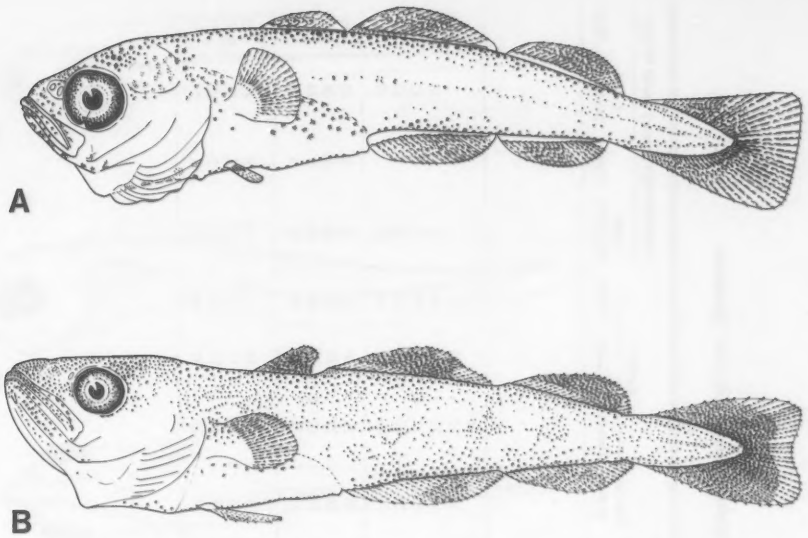


FIG. 2. *Eleginus gracilis*. A, larva 17.5 mm SL; B, early juvenile 27.2 mm SL.

present below pectoral fin buds. Additionally, melanophores form on base of pectoral fins in juveniles (Fig. 2B).

Preflexion larvae (approximately 4.7–6.3 mm) have two trunk pigment bars (Fig. 1A), characteristic of other gadid larvae in the Northeast Pacific Ocean (Matarese et al. 1981). Ventral stripe of anterior pigment bar contains 8–11 melanophores, occurs at 42–58% SL (covering myomeres 23–31), and is longer than dorsal stripe, which contains 5–7 melanophores (45–56% SL and myomeres 24–27). Ventral stripe of posterior bar longer than dorsal stripe. Ventral stripe, with 10–13 melanophores, occurs at 63–84% SL (myomeres 39–51), and dorsal stripe, containing 6–9 melanophores, occurs at 64–80% SL (myomeres 40–50). As larvae grow, dorsal and ventral stripes increase in length. In 7-mm larvae, pigment develops between ventral stripes to form continuous line of pigment from about myomeres 21 to 51, with hiatus at about myomeres 33–34 (Fig. 1B). Dorsal and ventral stripes of pigment persist through postflexion and early juvenile stages (about 17–27 mm). Ventral line consists of double row of melanophores on each side of body midline (Fig. 1D).

Lateral line series of melanophores initially develops in 7-mm larvae as a few pigment spots between dorsal and ventral stripes of posterior bar at about myomeres 42–43. These develop with growth of larvae and extend anteriorly of anus and posteriorly to procurrent caudal fin rays in early flexion larvae (Fig. 1E). They extend posteriorly to near hypural plates in late flexion larvae (Fig. 2A); ultimately this series becomes part of lateral body melanophores (Fig. 2B).

In postflexion larvae, melanophores cover dorso- and ventrolateral surface of postanal region (Fig. 2A) and ultimately cover entire lateral body (Fig. 2B). Pigment extends into dorsal, anal, and caudal fins in late flexion larvae and early juveniles (Fig. 2A); eventually these fins become covered with melanophores (Fig. 2B).

Osteology

Although only 18 larval and pelagic juvenile and 2 benthic juvenile *E. gracilis* were available to clear and stain for osteological examination, these samples were sufficient to provide a general understanding of the sequence of ossification in this species (Table 4).

Ossification occurs at later developmental stages than *M. proximus* (Matarese et al. 1981) and *T. chalcogramma* (J. R. Dunn, pers. obs.). Median and paired fins not developed until after notochord flexion complete. Certain head bones, fin pterygiophores and interneural bones, pectoral radials, and pelvic fin basipterygia not consistently ossified in largest pelagic juvenile (28.7 mm) examined. In early flexion larvae (about 11.7 mm), structures associated with feeding (maxillary, vomer, premaxillary, and dentary (with teeth on the latter three), upper pharyngeal teeth, and angular) begin to ossify, as do bones forming base of neurocranium (parasphenoid, basioccipital, and exoccipital). Additionally, cleithrum, supracleithrum, posttemporal, centra 1–4, and neural spines 1–5 have begun to ossify. In larger larvae (about 12–17 mm), additional head bones develop as do gill arches, branchiostegal rays, all vertebral centra, neural and haemal spines, and procurrent caudal fin rays. In postflexion larvae and pelagic juveniles (about 17–27 mm), median and paired fins commence ossification as do bones of caudal fin, some pleural and epipleural ribs, and additional head bones.

Parasphenoid, basioccipital, exoccipital, vomer, maxillary, angular, dentary, and premaxillary ossified in 11.7-mm larva; teeth develop on latter two bones (Table 4). In 12.5-mm specimen, mesethmoid, pterygoid, quadrate, hyomandibular, symplectic, interopercle, subopercle, preopercle, opercle, epihyal, ceratohyal, and retroarticular have begun to ossify. Additionally, in branchial region, urohyal, ceratobranchials

TABLE 4. Counts of meristic structures in larval and juvenile *Eleginus gracilis*. Specimen below solid line are juveniles.

Specimen length (mm SL)	Dorsal fin rays			Anal fin rays		Pectoral fin rays	Pelvic fin rays	Branchiostegal rays	Gill rakers			Teeth	
	1st	2nd	3rd	1st	2nd				Upper	Lower	Total	Premaxillary	Dentary
4.9													
5.5													
6.1													
9.4													
11.7												3	3
12.5								6		11	11	12	10
13.6								6		12	12	10	8
14.7								7		16	16	13	16
15.1								7		12	12	13	18
16.2								7		13	13	11	16
16.9		13	16	17	18	2	4	7		14	14	12	10
22.8	10	20	21	22	21	19	5	7	3	17	20	33	23
23.5	12	21	19	26	21	18	6	7	2	19	21	25	17
26.6	14	24	23	26	23	20	6	7	2	19	21	26	24
27.9	10	19	20	23	21	20	4	7	2	16	18	34	32
28.7	11	19	20	22	21	17	4	7	2	16	18	39	34
75.2[c]	15	20	24	23	22	20	6	7	3	17	20	70	43
85.3[c]	15	18	21	23	22	20	6	7	3	20	23	62	45

[a]Two neural spines present on preural centrum one.
[b]Two haemal spines present on preural centrum one.
[c]Benthic juveniles.

Specimens between broken lines are undergoing notochord flexion. Specimens

Teeth		Neural spines			Haemal spines	Centra			Procurrent and primary caudal fin rays			
									Upper		Lower	
Dentary	Vomer	Abdominal	Caudal	Total		Abdominal	Caudal	Total	procurrent	Primary	procurrent	Total
3		5		5		4		4				
10		22	34	56	34	22	30	52				
8		22	36	58	36	22	38	60	15		16	31
16		52	35	57	35	22	35	57	11		12	23
18		22	39	61	39	22	41	63	14		13	27
16		22	37	59	37	22	39	61	12		13	25
10		21	38	59	38	21	40	61	17	5	18	40
23	2	22	37	59[a]	36	22	38	60	24	5	26	55
17	3	22	36	58	36	22	38	60	23	5	24	52
24	4	21	36	57	37[b]	21	38	59	25	5	26	56
32	5	23	37	60[a]	37[b]	23	38	61	23	5	24	52
34	7	22	35	57	35	22	37	59	23	5	24	52
43	26	24	35	59	35	24	37	61	23	5	25	53
45	15	22	35	57	35	22	37	59	24	4	23	51

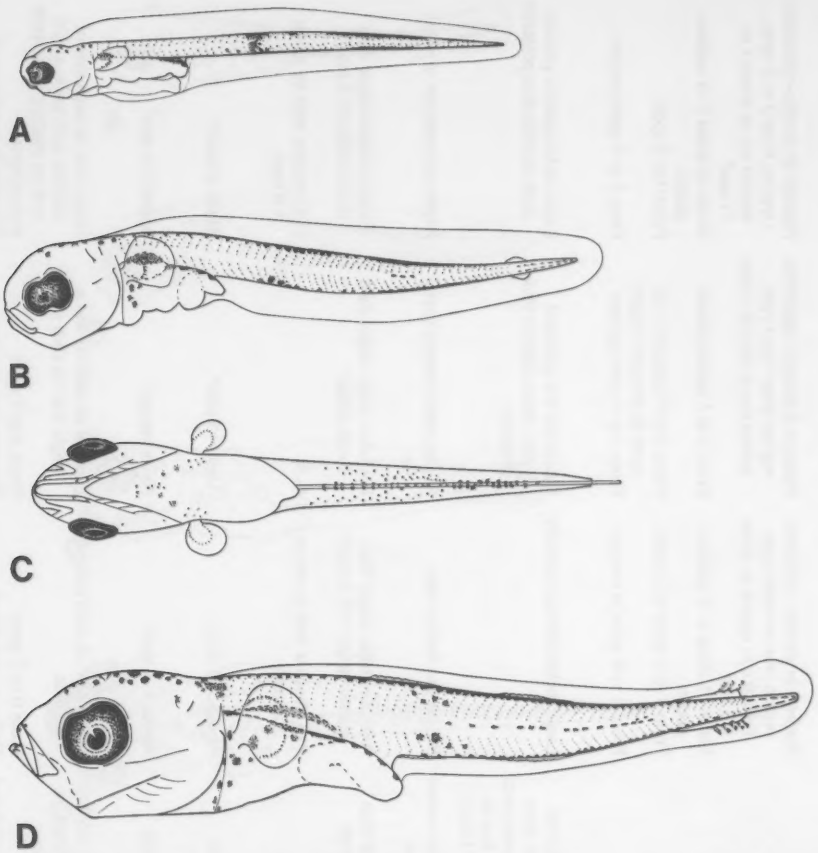


FIG. 3. Preflexion larvae of *Boreogadus saida*. A, 6.3 mm SL; B, 7.3 mm SL; C, 10.1 mm SL (ventral view); D, 10.1 mm SL.

1–5, ventral hypohyal, ventral branchial tooth plates, and branchiostegal rays 2–7 have begun to accept alizarin. Sphenotic, palatines, interhyal, opisthotic, pterotic, prootic, supraoccipital, lachrymal, frontals, entopterygoid, and all branchiostegal rays have begun to ossify in 13.6-mm specimen. Lateral ethmoids formed in 14.7-mm specimen, as have nasals, first two epibranchials, and upper hypohyals. Epiotic developed in 16.9-mm postflexion specimen. Alisphenoid, parietal, suborbital bones 2–5, basibranchials, and four extrascapulars ossified in 22.8-mm and larger specimens. Epibranchials 3 and 4 and hypobranchials 1–4, however, not consistently ossified in specimens 22.8–28.7 mm in length.

Cleithrum, supracleithrum, and dorsal fork of posttemporal formed in 11.7-mm specimen. Postcleithrum beginning to ossify in 14.7-mm larva. Coracoid and scapula beginning to ossify in 28.7-mm specimen, but pectoral radials not stained. Basipterygium ossifying in 27.9-mm but not 28.7-mm specimen. Pectoral and pelvic girdle ossified in 75.2-mm benthic juvenile.

Centra 1–4 and neural spines 1–5 ossified in 11.7-mm larva, whereas in 12.5-mm specimen, centra 1–32 and neural spines 1–35 stained red. All preural centra and all neural and haemal spines ossified in 13.6-mm larva, as are pleural ribs on centra 3 and 4. All centra and all neural and haemal spines ossified in 16.2-mm specimen. Pleural ribs on precaudal centra 3–17 and epipleural ribs on centra 3–6 developed in 22.8-mm specimen. Pleural ribs on all precaudal vertebrae (except centra 1 and 2) and epipleural ribs on vertebrae 3–10 ossified in 26.6-mm specimen. Parapophyses with expanded tips on precaudal vertebrae commencing with centrum 7 in benthic juveniles. First 4–6 haemal arches inflated in these specimens (Svetovidov 1948, 1965; Walters 1955).

Second and third dorsal fins and both anal fins partially ossified in 16.9-mm postflexion larva. First dorsal fin fully developed in 22.8-mm specimen. Insufficient specimens available for determining sequence of fin formation. Some pterygiophores and interneural bones partially ossified in 23.5-mm specimen, but not in larger pelagic juveniles. Procurrent caudal fin rays develop in larvae undergoing notochord flexion; "primary" (Markle 1982) caudal fin rays on superior hypural bone develop in postflexion larvae (Table 4). Caudal fin structure identical to that described for *M. proximus* by Matarese et al. (1981). Consists of anterior inferior hypural bone (hypural 1 of Materese et al. 1981) supporting one fin ray, posterior inferior hypural bone consistently supporting two fin rays, and superior hypural bone with five primary rays. Two

TABLE 5. Characters useful in separating larvae of *Eleginus gracilis*, *Boreogadus saida*, *proximus* at specific size ranges (data from this study except as noted).

Character	Size range (mm)	*E. gracilis*	*B. saida*
Pigment			
Head region			
Lateral head	5–13	1–6 spots in prootic–opisthotic region	None
Lateral dentary	6–12	Series of about 3–7 melanophores	None
Gular region	8–12	From 3 to 8 spots in a series	None
Anterior isthmus	7–13	About 5 to 10 spots covering region	None
Preanal region			
Ventral gut	4.4–13.5	Double row of small melanophores	Absent in larvae <10 mm; spots present anterior pectoral fins in larvae >10 mm
Lateral line	10–18	Begins anterior of vent	Begins under secon dorsal fin
Postanal region			
Length of ventral stripes (based on No. of melanophores)	4–6	Both longer than dorsal stripe	Both shorter than dorsal stripe
No. of myomeres from vertical of vent to anterior end of first ventral pigment stripe	4–6	4–6	5–7
Length at which dorsal pigment forms a continuous line	4–10	About 10 mm	About 7 mm
Length at which ventral pigment forms a continuous line	4–20	About 7 mm	About 10 mm
On ventral margin of body	10–15	In double row on each side of midline	Pigment on midlin and scattered on each side
Ventral caudal	7–11	None	None
Position of vent relative to dorsal fins	~15–20	Under second dorsal	Under second dors
No. of rays on superior hypural	>13	5	4

[a]From Matarese et al. (1981).

s saida, *Gadus macrocephalus*, *Theragra chalcogramma*, and *Microgadus*

ida	*G. macrocephalus*	*T. chalcogramma*	*M. proximus*
	Pigment in prootic–opisthotic region; one or more spots behind eye appear at about 4.5 mm	Pigment in prootic–opisthotic region; from 0 to 1 spot behind eye at about 9.0 mm	Pigment in prootic–opisthotic region; from 3 to 7 spots behind eye at about 5 to 11 mm[a]
	Series of about 4–8 melanophores	From 2 to 5 melanophores	Series of about 2–6 melanophores
	From 3 to 6 spots in a series	From 1 to 7 (usually 3–4) spots in midgular region	From 0 to 5 spots
	From 2 to 6 spots in a series	From 3 to 9 spots present	From 5 to 9 spots present
larvae ; spots nterior of fins in 10 mm	Large melanophores medially	Relatively few scattered spots, more anterior than posterior	Large melanophores present, more anterior than posterior
ler second n	Begins just before vent	Begins under second dorsal fin	Begins just anterior of vent[a]
er than ripe	Anterior stripe longer than dorsal stripe (<5.3 mm)[a]	Posterior stripe longer than dorsal stripe[a]	Anterior stripe longer than dorsal stripe (<5 mm)[a]
	1–3 (reaches vent by about 5.3 mm)	4–5	1–3 (reaches vent by about 5.0 mm)
m	About 5–6 mm[a]	About 13 mm[a]	About 13 mm[a]
nm	About 5–6 mm[a]	Never merge[a]	About 5–6 mm[a]
n midline ttered on e	Single row on each side of midline	Pigment on midline and a single row on each side	Single row on each side of midline anteriorly, single row on midline posteriorly
	From 0 to 2 spots	From 3 to 5 spots	Row of spots[a]
ond dorsal	Under second dorsal	Between first and second dorsal	Between first and second dorsal (ultimately under first dorsal)
	4[a]	4[a]	5[a]

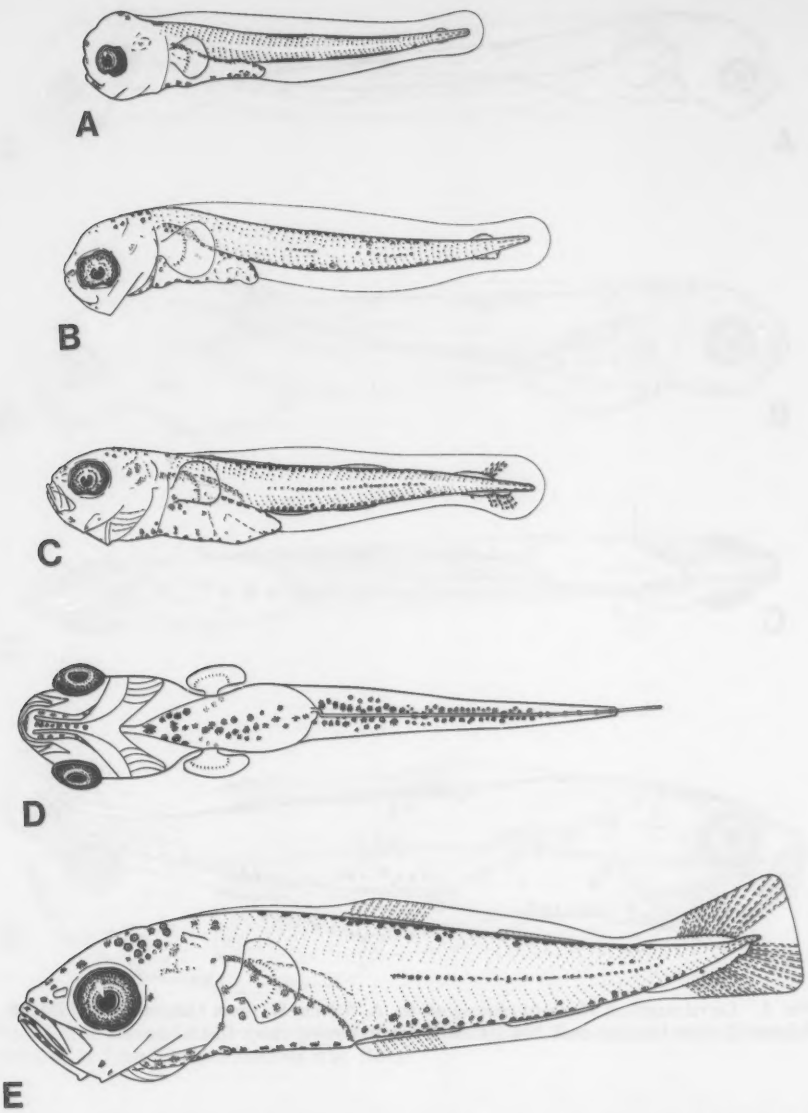


FIG. 4. Larval stages of *Gadus macrocephalus*. A, 4.4 mm SL; B, 5.6 mm SL (from Matarese et al. 1981); C, 8.5 mm SL (from Matarese et al. 1981); D, 11.0 mm SL (ventral view); E, 13.2 mm SL.

epurals, each supporting one fin ray, present, but uroneurals absent. Caudal fin associated with posteriormost 15–16 vertebrae. Pectoral and pelvic fins develop rays in postflexion larvae (Table 4). Ossification of pectoral fin rays from dorsal to ventral, and pelvic fin rays develop outward to inward.

Scales not developed on largest pelagic juvenile (28.7 mm) examined, but present on two benthic juveniles.

Criteria for Distinguishing Larvae of Cooccurring Gadids in the Northeast Pacific Ocean

In the Northeast Pacific Ocean (south of 70°N), certain size larvae of *E. gracilis* can be confused with larvae of other gadids in samples where they cooccur because of similarity in pigmentation and overlapping counts of meristic structures. Available literature on *E. gracilis* (Mukhacheva 1957) is inadequate to separate all sizes of this species from larvae of other cooccurring gadids. We summarize here and in Table 5 characters based on our original observations and the data of Matarese et al. (1981), which will distinguish preflexion, flexion, and postflexion larvae of *E. gracilis* from similar larvae of *B. saida*, *G. macrocephalus*, *T. chalcogramma*, and *M. proximus*.

Boreogadus saida

Preflexion larvae (4.7–10.5 mm) of *E. gracilis* best distin-

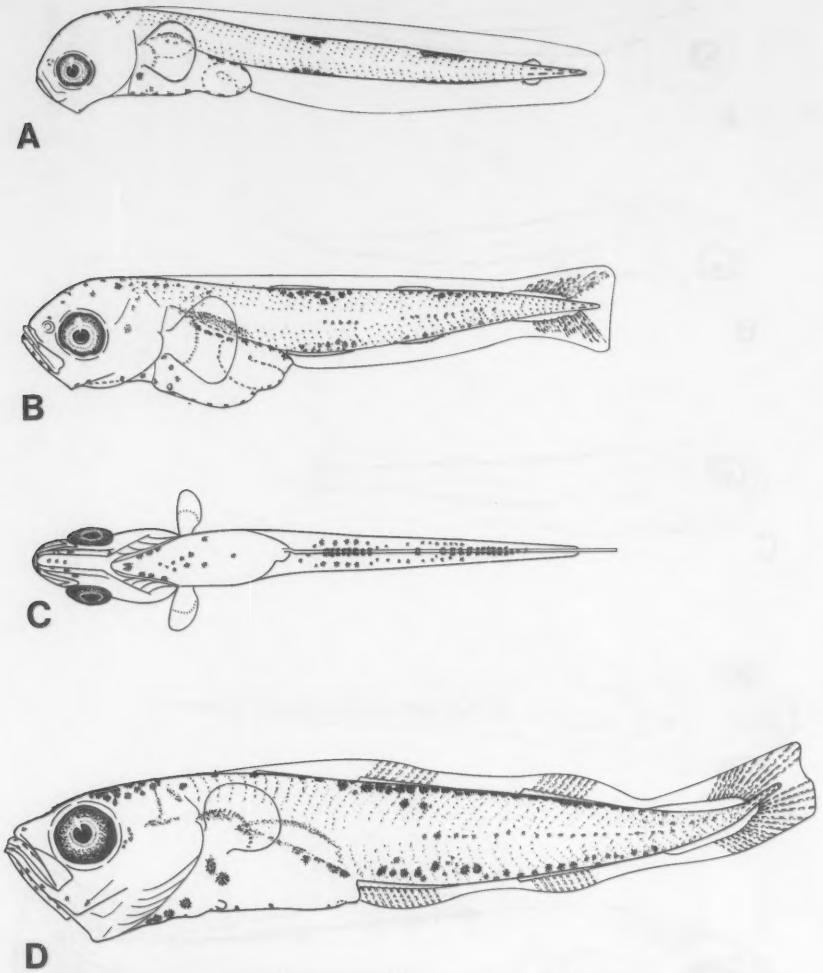


FIG. 5. Larval stages of *Theragra chalcogramma*. A, 6.2 mm SL (from Matarese et al. 1981); B, 9.8 mm SL (from Matarese et al. 1981); C, 10.1 mm SL (ventral view); D, 13.7 mm SL.

guished from *B. saida* by higher myomere counts (Table 2), extent of ventral gut pigment, and relative position and differences in lengths of postanal pigment bars. Two rows of pigment spots present on ventral gut in *E. gracilis*, but gut pigment absent in *B. saida*. In *E. gracilis* larvae (4.7–6.3 mm), ventral stripes of anterior and posterior pigment bars longer (covering myomeres 20–30 and 33–51, respectively) than dorsal stripes (myomeres 22–29 and 35–50) (Fig. 1A). In similar size *B. saida* larvae, however, dorsal stripe of two postanal pigment bars longer (myomeres 20–29, with frequent hiatus in pigment at myomeres 25, 26–27 and 32–50, 51) than ventral stripe (myomeres 20–25 and about 38–51) (Fig. 3A). Additionally, number of melanophores in ventral stripe of anterior pigment bar and dorsal stripe of posterior bar differs between the two species (*E. gracilis* has 8–11 and 5–9, respectively, and *B. saida* has 4–5 and 16–20). In *E. gracilis* larvae, ventral pigment stripes of two postanal bars form continuous line of pigment at approximately 7 mm (Fig. 1B), before stripes of dorsal bars become continuous. In *B. saida* larvae, two dorsal stripes become continuous at about 7 mm; ventral stripes remain separate until about 10 mm (Fig. 3B, 3C). *Eleginus gracilis* larvae have pigment on dentrary and diagnostic internal pigment in prootic–opisthotic region; *B. saida* has scattered pigment spots only on top of head. Preflexion larvae of *B. saida* in Bering and Chukchi seas lack posterior gut pigment described for North Atlantic Ocean specimens by Schmidt (1905) and Russell (1976).

In flexion larvae (about 10–17 mm), *E. gracilis* separated from *B. saida* by the following: *E. gracilis* has pigment on gular and anterior isthmus region; ventral gut pigment, generally in two rows (Fig. 1D); lateral line pigment extending anterior to posterior margin of vent; ventral postanal pigment in double row

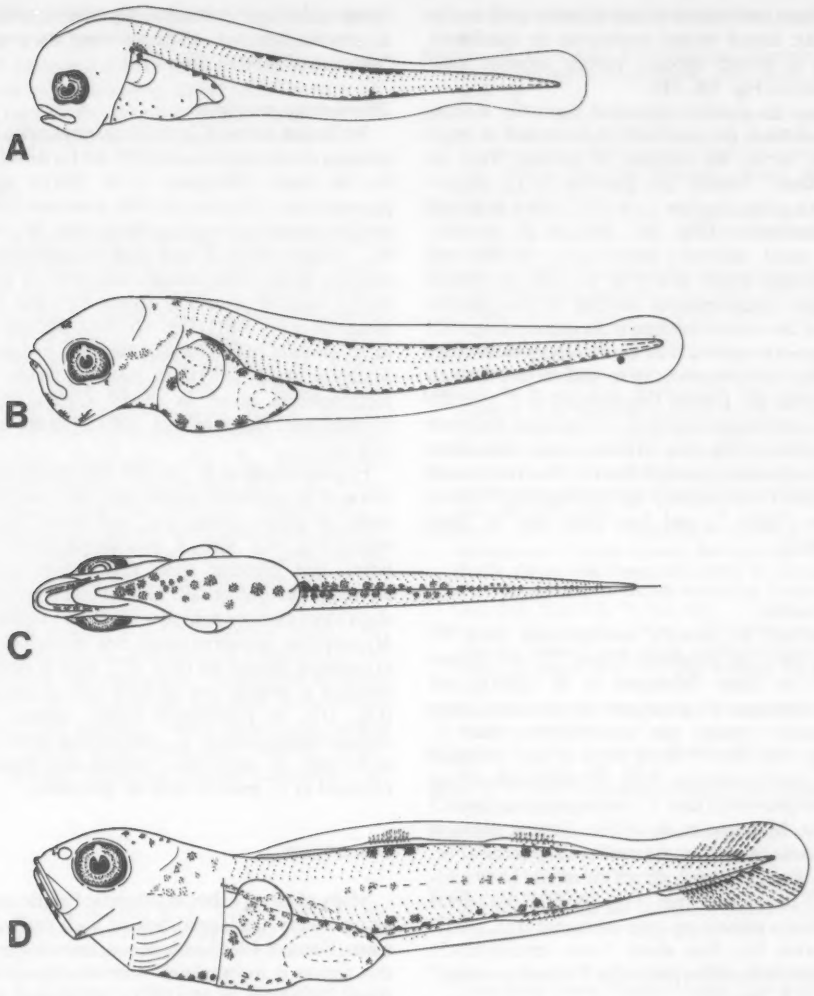


FIG. 6. Larval stages of *Microgadus proximus*. A, 3.6 mm SL; B, 5.7 mm SL; C, 8.4 mm SL (ventral view); D, 10.7 mm SL (from Matarese et al. 1981).

on each side of midline of body; superior hypural bone supports five primary rays in larvae longer than 13 mm. In contrast, *B. saida* lacks pigment on isthmus, gular region, and gut pigment posterior of pectoral fins, has ventral postanal pigment on body midline and scattered melanophores anteriorly on each side of midline (Fig. 3C), has lateral line of pigment terminating before vent (Fig. 3D), and has four primary rays on superior hypural bone in specimens longer than 13 mm (Table 2). With further growth, *B. saida* acquires pigment spots on gular region and occasionally on posterior portion of isthmus; lateral walls of gut become densely pigmented. Postflexion larvae and early juveniles (~18–28 mm) of two species best separated on extent of gut and lateral line pigment, number of rays on superior hypural bone, and number of rays in second dorsal fin, first anal fin, and number of gill rakers (Table 2).

Gadus macrocephalus

Preflexion larvae of *E. gracilis* best distinguished from similar stage larvae of *G. macrocephalus* using counts of meristic structures and evaluation of pigment patterns. *Gadus macrocephalus* larvae have 49–56 myomeres (Matarese et al. 1981) and larger and fewer ventral gut melanophores (Fig. 4A) than *E. gracilis* (Fig. 1A). In preflexion larvae (<5 mm) beginning of ventral stripe of anterior postanal bar (covering myomeres 16–26, Matarese et al. 1981) in *G. macrocephalus* is 1–3 myomeres posterior of vent and about 4–6 myomeres in *E. gracilis* (Fig. 1A; 4A). Ventral postanal stripes in each pigment bar in *E. gracilis* contain 8–11 and 10–13 melanophores, respectively, but *G. macrocephalus* has about 8 and 10 such melanophores (Matarese et al. 1981). Ventral postanal pigment stripes in *G. macrocephalus* form continuous line in larvae

5–6 mm, whereas these two stripes remain separate until nearly 7 mm in *E. gracilis*; dorsal stripes continuous in specimens 5–6 mm in length in former species, remain separate until 10 mm in latter species (Fig. 4B, 1B).

In flexion larvae, *E. gracilis* separated from *G. macrocephalus* on basis of head, gut, and body pigment and in larger (>13 mm) flexion larvae by number of primary rays on superior hypural bone. Ventral gut pigment in *G. macrocephalus* consists of relatively few (~8–12), rather scattered large stellate melanophores (Fig. 4C, 4D); in *E. gracilis*, melanophores are small, relatively numerous (~16–38), and arranged in approximate double row (Fig. 1C, 1D). In ventral view, postanal series melanophores consists of two parallel rows on each side of the ventral midline in *E. gracilis* (Fig. 1D) and only a single row on each side in *G. macrocephalus* (Fig. 4D). In both species, vent lies posterior to vertical line through origin of second dorsal fin. Lateral line pigment in *E. gracilis* extends anteriad to terminus of vent (Fig. 1E) but does not reach vent in *G. macrocephalus* (Fig. 4E). In larvae longer than about 13 mm, *E. gracilis* also distinguished from *G. macrocephalus* based on possession of five primary rays on superior hypural element in former (Table 2) and four such rays in latter (Matarese et al. 1981).

Theragra chalcogramma

Preflexion larvae of *E. gracilis* distinguished from *T. chalcogramma* on basis of myomere counts (57–64 former (Table 2); 48–52 for latter (Matarese et al. 1981)) and differences in pigmentation. *Eleginus gracilis* possesses more numerous and smaller ventral gut melanophores than *T. chalcogramma* (Fig. 1A, 5A). Ventral stripe of each postanal pigment bar in *E. gracilis* contains more melanophores (about 8–11 and 10–13, respectively) than *T. chalcogramma* (about 5 and 7, respectively, Matarese et al. 1981). Ventral pigment stripes form continuous line in 7-mm larvae of *E. gracilis* (Fig. 1B), whereas in *T. chalcogramma*, stripes on ventral body midline remain separate until 10–12 mm (Fig. 5B, 5D), but lateral portion of stripes always remain separate (Matarese et al. 1981). Additionally, in larvae less than about 7 mm, several (2–5) ventral caudal melanophores often present in *T. chalcogramma*, but usually absent in *E. gracilis*.

Flexion larvae of *E. gracilis* also distinguished from similar larvae of *T. chalcogramma* in that latter has two to five pigment spots just posterior to eye margin, while such pigment is lacking in *E. gracilis* (Fig. 1C, 1E, 5D). Additionally, lateral line pigment extends anterior to vent in *E. gracilis* (Fig. 1C, 1E), but terminates 5–6 myomeres posterior to vent in *T. chalcogramma* (Fig. 5D). Ventral body pigment in *T. chalcogramma* in a single row on each side of body midline (Fig. 5C), as opposed to double row in *E. gracilis* (Fig. 1D). Postflexion larvae and pelagic juveniles of two species best separated on basis of position of vent relative to second dorsal fin, number of rays on superior hypural bone, and overall pigmentation. Vent in *E. gracilis* lies under second dorsal fin; in *T. chalcogramma* it ends between first and second dorsal fin. *Eleginus gracilis* has five rays articulating with superior hypural bone (Table 2); *T. chalcogramma* has four (Matarese et al. 1981). Pigmentation generally increases with growth of larvae of both species and becomes somewhat similarly distributed. In postflexion larvae to about 22 mm, lateral line pigment persists and length of pigment line can aid in distinguishing the two species. In larger larvae and pelagic juveniles, pigment is, subjectively, lighter in *E. gracilis* than in *T. chalcogramma* and consists of somewhat "checkered" pattern (Fig. 2B).

Microgadus proximus

Preflexion larvae *E. gracilis* distinguished from *M. proximus* on basis of myomere counts (57–64 for former (Table 2); 54–58 for the latter (Matarese et al. 1981)) and differences in pigmentation. *Eliginus gracilis* possesses more numerous and smaller ventral gut melanophores than *M. proximus* (Fig. 1D, 6C). Ventral stripe of each postanal pigment bar in *E. gracilis* contains more melanophores (about 8–11 and 10–13, respectively) than *M. proximus* (about 4–5 and 7–8, respectively, Matarese et al. 1981) (Fig. 1A, 6A). Second bar more posterior in *E. gracilis* (63–84% SL) than *M. proximus* (59–72% SL, Matarese et al. 1981). In smallest larvae of *M. proximus*, melanophores occur in caudal region posterior to second pigment bar (Matarese et al. 1981), but are usually absent in *E. gracilis*.

Flexion larvae of *E. gracilis* also distinguished from similar larvae of *M. proximus* in that latter has fewer and larger pigment spots on body, ventral gut, and dorsal and ventral postanal region (Fig. 6C). Also, *E. gracilis* has many more, and smaller, lateral line pigment spots that extend posteriorly to short distance from end of tail. Lateral line pigment on *M. proximus* stops short distance behind second bar. Ventral body pigment in *M. proximus* in uneven single row on each side of body midline to posterior second bar (Fig. 6C), then in single midline row, as opposed to double row on each side of midline in *E. gracilis* (Fig. 1D). In postflexion larvae, ventral gut pigment best distinguishing feature: *E. gracilis* has finer and more pigment spots than *M. proximus*. Lateral line pigment is more pronounced in *E. gracilis* than *M. proximus*.

Discussion

Study of larval fishes in subarctic Pacific and North American arctic waters has lagged behind such studies in other oceanic areas (Kendall 1981) and, hence, knowledge of gadid larvae in this region is incomplete. With this report and a predecessor paper (Matarese et al. 1981), all gadine (sensu Svetovidov 1948) larvae occurring in oceanic waters contiguous to North America from southern California to the Chukchi Sea (to 70°N) can now be specifically identified.

In addition to *E. gracilis* and *B. saida*, three other nominal species of gadids occur in North American arctic waters from about 160 to 66°W (north of 65°N): the toothed cod, *A. borisovi*, the polar cod, *A. glacialis*, and the ogac, *G. ogac* (Nielsen and Jensen 1967; Boulva 1972; Quast and Hall 1972; McAllister 1984). Larvae of *A. borisovi* were partially described by Zviagina (1961), but the description is inadequate to identify *A. borisovi* larvae or to differentiate them from *A. glacialis*, whose larvae are not known. Additionally, larvae of *G. ogac* are poorly known and undescribed (e.g. Buchanan and Foy 1980).

Counts of meristic structures overlap among *A. borisovi*, *A. glacialis*, and *G. ogac* (Svetovidov 1948; Boulva 1972; this study) and hence are of only limited utility in discriminating among larvae of these three species. If preflexion gadid larvae are encountered in North American arctic waters that do not fit the descriptions of either *E. gracilis* or *B. saida*, they cannot at present be specifically identified. However, flexion larvae, in

which the caudal fin has developed, can be assigned to either *Arctogadus* species or *G. ogac*, based on the structure of this fin. Both species of *Arctogadus* have four rays on the superior hypural bone and one ray articulating with hypural bone 2; *G. ogac* also has four rays on the superior hypural bone, but two rays are present on hypural bone 2 (this study).

Acknowledgments

We thank A. C. Matarese and A. W. Kendall Jr. (NWAFC) for helpful discussions and constructive review of this manuscript. For loan of specimens, radiographs, and/or helpful correspondence, we thank W. Eschmeyer, California Academy of Sciences, San Francisco, CA; J. Long, Oregon State University, Corvallis, OR; D. McAllister and D. Faber, National Museum of Canada, Ottawa, Ont; T. Pietsch and T. English, University of Washington, Seattle, WA; L. Barton, Alaska Department of Fish and Game (ADFG), Anchorage, AK; K. Frost, ADFG, Fairbanks, AK; N. Wilimovsky, University of British Columbia, Vancouver, B.C.: B. Wing, NWAFC, Juneau, AK; A. Sekerak, LGL Ltd., Sidney, B.C.; and R. Ratynski, Freshwater Institute, Winnipeg, Man. Particular appreciation is extended to Dr Rita Horner, Seattle, for her loan of extensive collections of gadid larvae from the Bering and Chukchi seas. Research conducted by R. Horner, T. English, and the authors, which resulted in the collection of some of the specimens reported upon herein, was partially supported by the Outer Continental Shelf Environmental Assessment Program (OCSEAP), NOAA. This manuscript benefited from critical reviews by D. Cohen, Los Angeles County Museum of Natural History; M. Fahay, Sandy Hook Laboratory (NMFS), Highlands, NJ; and D. Markle, Huntsman Marine Laboratory, St. Andrew's, N.B.

References

AHLSTROM, E. H., J. L. BUTLER, AND B. Y. SUMIDA. 1976. Pelagic stromateoid fishes (Pisces, Perciformes) of the eastern Pacific: kinds, distributions, and early life histories and observations on five of these from the northwest Atlantic. Bull. Mar. Sci. 26: 285–402.

AHLSTROM, E. H., AND R. C. COUNTS. 1955. Eggs and larvae of the Pacific hake, *Merluccius productus*. U.S. Fish. Wildl. Serv. Fish. Bull. 56: 295–329.

BATES, R. D., AND J. CLARK. 1983. Ichthyoplankton off Kodiak Island and the Alaska peninsula during spring 1981. U.S. Dep. Commer. Natl. Mar. Fish. Serv. Northw. Alaska Fish. Cent. Proc. Rep. 83–09: 106 p.

BOULVA, J. 1972. Morphometrics of three sympatric arctic codfishes of the genera *Arctogadus* and *Gadus*. J. Fish. Res. Board Can. 29: 243–249.

BUCHANAN, R. A., AND M. G. FOY. 1980. Offshore Laborador biological studies, 1979: plankton, nutrients, chlorophyll, phytoplankton, and ichthyoplankton. Part 1. Atlantic Biological Services Ltd., P.O. Box 13248, Stn. A, 306 Kenmount Road, St. Johns, Nfld. A1B 4A5. 123 p. (Prepared for Total Eastcan Explorations Ltd., Calgary, Alta.)

DINGERKUS, G., AND L. D. UHLER. 1977. Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. Stain Technol. 52: 229–232.

DUNN, J. R. 1983. The utility of developmental osteology in taxonomic and systematic studies of teleost larvae: a review. U.S. Dep. Commerc. NOAA Tech. Rep. NMFS Circ. 450: 19 p.

GORBUNOVA, N. N. 1954. The reproduction and development of walleye pollock, *Theragra chalcogramma* (Pallas). Akad. Nauk SSSR Tr. Inst. Okeanol. 11: 132–195. (Engl. transl. U.S. Dep. Commer., Natl. Mar. Fish. Serv., Northw. Alaska Fish. Cent., Seattle, WA)

HARRINGTON, R. W. JR. 1955. The osteocranium of the American cyprinid fish, *Notropis bifrenatus*, with an annotated synonomy of teleost skull bones. Copiea 1955: 267–290.

HART, J. L. 1973. Pacific fishes of Canada. Fish. Res. Board Can. Bull. 180: 740 p.

KENDALL, A. W. JR. 1981. Early life history of eastern North Pacific fishes in relation to fisheries investigations. Univ. Wash. Sea Grant Tech. Rep. 81-3: 7 p.

KENDALL, A. W. JR., J. R. DUNN, R. J. WOLOTIRA JR., J. H. BOWERMAN JR., D. B. DEY, A. C. MATARESE, AND J. E. MUNK. 1980. Zooplankton, including ichthyoplankton and decapod larvae of the Kodiak shelf. U.S. Dep. Commer. Natl. Mar. Fish. Serv. Northw. Alaska Fish. Cent. Proc. Rep. 80-8: 393 p.

KHALDINOVA, N. A. 1936. Study of spawning, eggs, and larvae of *Eleginus (Gadus) navaga* Pall. Zool. Zh. 15: 321–339. (In Russian, English summary).

KOZLOV, B. M. 1952. Some observations on development of navaga eggs. Izv. Tikhookean. Nauchno-issled. Inst. Rybn. Khoz. Okeanogr. 37: 255. (In Russian, Engl. Transl. U.S. Dep. Commer., Natl. Mar. Fish. Serv., Northw. Alaska Fish. Cent. 2 p.)

KUSMIN-KARAWAJEW, G. A. 1930. Biology of the white sea navaga. Tr. Nauchno. Inst. Rybn. Khoz. 4: 83–86. (In Russian)

LAROCHE, W. A., AND S. L. RICHARDSON. 1981. Development of larvae and juveniles of the rockfishes *Sebastes entomelas* and *S. zacentrus* (family Scorpaenidae) and occurrence off Oregon, with notes on head spines of *S. mystinus*, *S. flavidus*, and *S. melanops*. Fish. Bull. U.S. 79: 231–257.

MARKLE, D. F. 1982. Identification of larval and juvenile Canadian Atlantic gadoids with comments on the systematics of gadid subfamilies. Can. J. Zool. 60: 3420–3438.

MATARESE, A. C., S. L. RICHARDSON, AND J. R. DUNN. 1981. Larval development of Pacific tomcod, *Microgadus proximus*, in the northeast Pacific Ocean with comparative notes on larvae of walleye pollock, *Thereagra chalcogramma*, and Pacific cod, *Gadus macrocephalus* (Gadidae). Fish. Bull. U.S. 78: 923–940.

MATTSON, C. R., AND B. L. WING. 1978. Ichthyoplankton composition and plankton volumes from inland coastal waters of southeastern Alaska, April–November 1972. U.S. Dep. Commer. NOAA Tech. Rep. SSRF-723: 11 p.

MCALLISTER, D. E. 1984. Distributional atlas of marine fishes of arctic Canada. Syllogus. (In press)

MORROW, J. E. 1980. The freshwater fishes of Alaska. Alaska Northwest Publ. Co., Anchorage, AK. 248 p.

MUJIB, K. A. 1967. The cranial osteology of the Gadidae. J. Fish. Res. Board Can. 24: 1315–1375.

MUKHACHEVA, V. A. 1957. Notes on the development of the far eastern navaga (*Eleginus gracilis* (Tilesius)). Akad. Nauk SSSR Tr. Inst. Okeanol. 20: 356–370. (Engl. transl., Am. Inst. Biol. Sci., 1959: 291–302)

MUKHACHEVA, V. A., AND O. A. ZVIAGINA. 1960. Development of the Pacific cod, *Gadus morhua macrocephalus* (Tilesius). Akad. Nauk SSSR Tr. Inst. Okeanol. 31: 145–165. (Engl. transl., Fish. Res. Board Can. Transl. Ser. 393)

NIELSEN, J. G., AND J. M. JENSEN. 1967. Revision of the arctic cod genus *Arctogadus* (Pisces, Gadidae). Medd. Gronl. 184(2): 1–29.

PONOMAREVA, L. A. 1949. Eggs and fry of fishes on the Kara Sea. Tr. Nauchno. Inst. Rybn. Khoz. Okeanogr. 17: 189–205. (In Russian)

QUAST, J. C., AND E. L. HALL. 1972. List of fishes of Alaska and adjacent waters with a guide to some of their literature. U.S. Dep. Commer. NOAA Tech. Rep. NMFS SSRF-658: 47 p.

RASS, T. S. 1949. The composition of fish fauna of the Barents Sea and the systematical characters of the fish eggs and larvae. Tr. Nauchno. Inst. Rybn. Khoz. Okeanogr. 17: 7–65. (In Russian)

RATYNSKI, R. A. 1983. Mid-summer ichthyoplankton populations of Tuktoyaktuk Harbour, N.W.T. Can. Tech Rep. Fish. Aquat. Sci. 1218: 21 p.

RUSSELL, F. S. 1976. The eggs and planktonic stages of British marine fishes. Academic Press, London. 534 p.

SCHMIDT, J. 1905. The pelagic post-larval stages of the Atlantic species of *Gadus*. Part 1. Meddr. Kommn. Havunders. Ser. Fiskeri 1, Nr 4: 77 p.

SVETOVIDOV, A. N. 1948. GADIFORMES. Akad. Nauk SSSR Zool. Inst. Fauna SSSR, Ryby, 9(4), N.S. 34: 221 p. (Engl. transl., Israel Program Sci. Transl., 1962. 304 p.)

1965. Specific differences between the european and Pacific navagas (*Eleginus navaga* and *E. gracilis*) and the taxonomic position of the navaga of Arctic Alaska and Canada. Zool. Zh. 44: 220–227. (Engl. transl. available as TT69-59036 from U.S. Dep. Commer., Natl. Tech. Inf. Serv., Springfield, VA)

UCHIDA, K., S. IMAI, S. MITO, S. FUGITA, M. UENO, Y. SHOMITA, T. SENTA, M. TAHUKU, AND Y. DOTU. 1958. Studies on the eggs, larvae and juveniles of Japanese fishes. Kyushu Univ. Fac. Agric. Fish. Dep. 2d Lab.

Ser. 1: 85 p. (Engl. transl. available from U.S. Dep. Commer., Natl. Mar. Fish. Serv., Northw. Alaska Fish. Cent., Seattle, WA, 1961, p. 26–27, 30–31, and 65)

WALDRON, K. D. 1981. Ichthyoplankton, p. 471–493. *In* D. W. Hood and J. A. Calder [ed.] The eastern Bering Sea shelf: oceanography and resources. Vol. I. U.S. Government Printing Office, Washington, DC.

WALTERS, V. 1955. Fishes of western Arctic America and eastern Arctic Siberia. Bull. Am. Mus. Nat. Hist. 106: 261–368.

WOLOTIRA, R. J. JR., T. M. SAMPLE, AND M. MORIN JR. 1977. Demersal fish and shellfish resources of Norton Sound, the southeastern Chukchi Sea, and adjacent waters in the baseline year 1976. Northw. Alaska Fish. Cent. Proc. Rep.: 292 p.

YUSA, T. 1954. On the normal development of the fish, *Theragra chalcogramma* (Pallas), Alaska pollock. Bull. Hokkaido Reg. Fish. Res. Lab. 10: 1–15. (In Japanese, English summary)

ZVIAGINA, O. A. 1961. Data on the propagation and development of fish of Laptev Sea. 1. East-Siberian cod (*Arctogadus borisovi*, Gadidae). Akad. Nauk SSSR. Tr. Inst. Okeanol. 43: 320–327. (Engl. transl., Fish. Res. Board Can. Transl. Ser. 1278)

Spawning Site Water Chemistry and Lake Trout (*Salvelinus namaycush*) Sac Fry Survival during Spring Snowmelt

J. M. Gunn

Ontario Ministry of Natural Resources, P.O. Box 3500, Station A, Sudbury, Ont. P3A 4S2

W. Keller

Ontario Ministry of the Environment, 199 Larch Street, Sudbury, Ont. P3E 5P9

Gunn, J. M., and W. Keller. 1984. Spawning site water chemistry and lake trout (*Salvelinus namaycush*) sac fry survival during spring snowmelt. Can. J. Fish. Aquat. Sci. 41: 319–329.

During the spring of 1982, lake trout (*Salvelinus namaycush*) sac fry were incubated at a spawning bed in a pH 5.7 lake with a history of lake trout recruitment failure. Four short episodes of substantial pH depression occurred at the spawning site. Observed sac fry mortalities (18%) occurred primarily during the longest depression (5 d at pH 4.5–5.0), which coincided with maximum surface runoff and peaks in concentrations (~50 μg/L) of inorganic (monomeric) Al. Although most mortalities were coincident with low pH and elevated inorganic Al concentrations, the high survival (82%) demonstrated that under natural conditions most sac fry could tolerate pH <5.0 and inorganic Al concentrations of 40–50 μg/L for at least 5 d. Substantially higher concentrations of inorganic Al (~80 μg/L) were observed in the interstitial waters of the spawning rubble than in ambient waters, which indicated that fry within a spawning substrate may be subjected to more toxic conditions than test fry in incubators above the substrate surface.

Au printemps 1982, des alevins de touladi (*Salvelinus namaycush*) vésiculés ont été incubés sur frayère d'un lac à pH 5,7 où le recrutement de cette espèce avait connu, dans le passé, de nombreux échecs. Il y eut, cette année-là à ce site, quatre courtes périodes pendant lesquelles le pH a baissé de façon substantielle. Les mortalités d'alevins (18 %) survinrent en grande partie pendant la période de bas pH (5 d à des pH de 4,5–5,0), qui coïncida avec le maximum de ruissellement de surface et des pics de concentrations (~50 μg/L) de Al inorganique (monomérique). Bien que la plupart des mortalités aient coïncidé avec un bas pH et des concentrations élevées de Al inorganique, le pourcentage de survie élevé (82 %) démontre que, dans des conditions naturelles, la plupart des alevins vésiculés peuvent tolérer des pH <5,0 et des concentrations de Al inorganique de 40–50 μg/L pendant au moins 5 d. On a observé des concentrations beaucoup plus fortes de Al inorganique (~80 μg/L) dans les eaux interstitielles de la pierraille des frayères que celles des eaux ambiantes, ce qui indique que les alevins dans un substrat particulier d'une frayère peuvent être exposés à des conditions plus toxiques que des alevins expérimentaux dans des incubateurs situés au-dessus de la surface du substrat.

Received June 24, 1983
Accepted November 3, 1983

Reçu le 24 juin 1983
Accepté le 3 novembre 1983

Episodic fluctuations in pH, often associated with snowmelt (Hagen and Langeland 1973; Hultberg 1977; Jeffries et al. 1979; Scheider et al. 1979; and others) can occur in poorly buffered lakes receiving high acid loadings. For fall spawning fish species, such as lake trout (*Salvelinus namaycush*) and brook trout (*S. fontinalis*), the timing of hatch, yolk absorption, and emergence may subject progeny to depressed pH levels produced by snowmelt (Jeffries et al. 1979; Gunn and Keller 1981; Peterson et al. 1982). Spawning sites are often shallow and located along shorelines, further increasing the chance that the relatively immobile larvae are exposed to acid meltwater. The high sensitivity of early life stages to low pH (Schofield 1976; Haines 1981) and the finding that natural populations generally decline through recruitment failure rather than mass mortality (Muniz and Leivestad 1980a; Haines 1981) provide further evidence that meltwater impacts may be responsible for the decline of many fish species affected by acidification. However, the mechanism of fish toxicity during low pH episodes may not simply involve H^+. Aluminum toxicity has been implicated in fish mortality under acidic conditions (Schofield and Trojnar 1980). Very little data exist to test laboratory-derived functional relationships between water quality (eg. pH, Al) and fish response, particularly for episodic acid meltwater conditions.

Acidification appears to have caused the extinction of ~60 indigenous lake trout populations near Sudbury (Gunn 1982). The acidification of Sudbury area lakes and resultant declines in fish populations have been associated with atmospheric emissions from the Sudbury metal smelting industry (Beamish and Harvey 1972; Keller et al. 1980). These population losses usually consist of total extinction, which, according to historical data, occurred mainly between 1950 and 1970. However, in a few cases very small remnant populations of large, old fish still exist in low pH (< 5.5) lakes (Beamish et al. 1975; Kelso and Gunn 1982). The spawning site of one such remnant lake trout population formed the basis of our study of the role of chemical changes during snowmelt on lake trout recruitment.

Study Lake

Whitepine Lake (47°17′N, 80°50′W) is a 67-ha single basin headwater lake (elevation 412 m) located 90 km north of

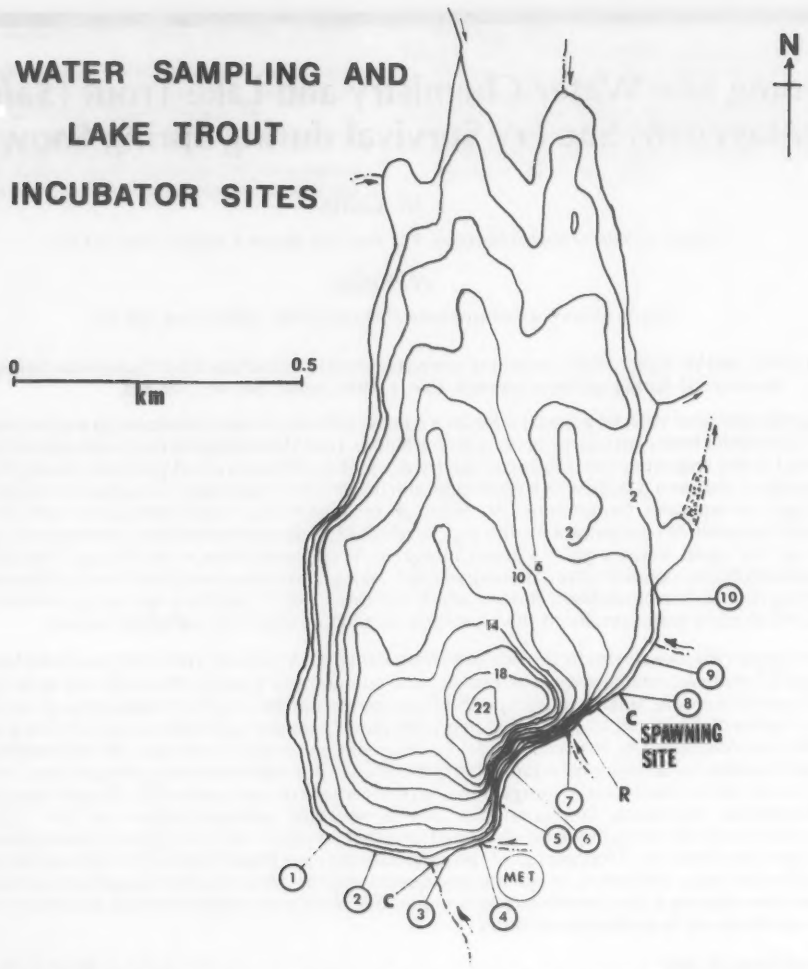


FIG. 1. Whitepine Lake, showing the locations of experimental incubators (at the spawning site), control incubators (C), water sampling stations (1–10), the runoff collection site (R), and the meteorological station (MET).

Sudbury, Ont. Based on averages of biweekly midlake measurements from the ice-free period of 1981 (W. Keller, unpubl. data) the lake can be characterized as dilute, (conductivity 35 μS/cm) oligotrophic (total P 6 μg/L), and intermediately acidic (pH 5.7). Calcium (125 μeq/L) and SO_4^{2-} (227 μeq/L) are the dominant cation and anion, respectively. Low concentrations of Cu and Ni (< 2 μg/L) indicate little present effect of metal emissions from the Sudbury smelting complex. Lakewater concentrations of Al (49 μg/L), a metal known to be mobilized from watersheds (Johnson 1979) and lake sediments (Schindler et al. 1980) under acidic conditions, are comparable with values reported for lakes in south-central Ontario (Dillon et al. 1978, 1980). Maximum and mean depths are 22 and 5.9 m, respectively. The lake has 4.7 km of shoreline, with the clean gravel and rubble sites characteristic of lake trout spawning areas occurring predominantly along the windswept south and southeast shores (Fig. 1). Although it is relatively small and shallow for a lake trout lake (Martin and Olver 1976), temperature and dissolved oxygen conditions are suitable for the species. During late summer stratifiction, the thermocline is located between 8 and 12 m and the hypolimnion remains below 8°C. The waters above 16 m maintain > 5 mg/L dissolved oxygen throughout stratification.

The indigenous fish community exhibits many of the characteristics of acid-stressed systems. Sensitive species such as lake trout, burbot (*Lota lota*), and white sucker (*Catostomus commersoni*) are extremely scarce and consist only of large adults, while yellow perch (*Perca flavescens*) are very abundant and show no signs of recruitment failure, consistent with observations in other acid-stressed lakes (Beamish et al. 1975; Kelso and Gunn 1982). Based on tag–recapture data, the native lake trout brood stock consisted of ~ 10 individuals in 1981. From the age of the native trout (~ 15 yr) the last successful spawning occurred approximately 1970, about the same time that angling quality declined (J. M. Gunn, unpubl. data).

Whitepine Lake also contains some hatchery-reared lake trout. In the fall of 1980 the lake was stocked with 800 adipose-fin-clipped yearlings from Tarentorous Hatchery (Sault

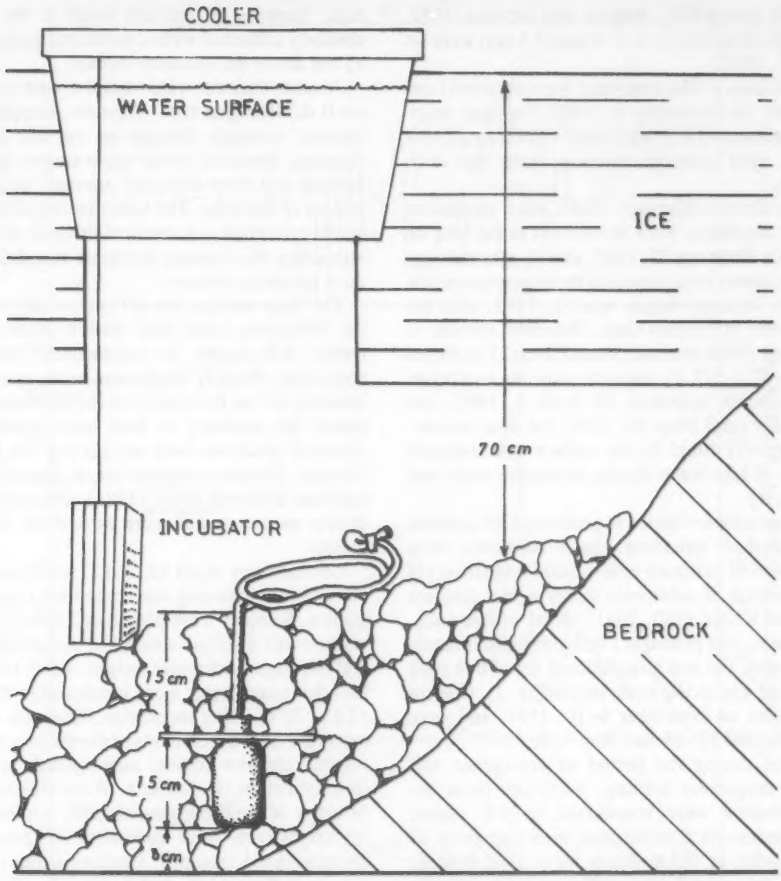


FIG. 2. Experimental setup at the Whitepine Lake spawning bed, showing incubators, interstitial water sampler, and bottomless cooler installed to minimize refreezing of ice cover between visits and the inflow of surface meltwater.

Ste. Marie, Ont.). The stocking was repeated in the fall of 1981 with fin-clipped 2+ trout. Subsequent test netting showed good survival and growth of the stocked fish.

Approximately 30% of the watershed's forest cover was cut or later burned in a 1975 fire; however, a band of shrubs and trees remains along most of the burned portion of the shoreline. There is no evidence of severe water level fluctuations or excess erosion or siltation in the past. Few human disturbances currently exist in the 328-ha watershed. Our small field station is the only building. Road access is seasonal and very difficult. The lake has been closed to angling since the fall of 1980.

Spawning Site

The location of the only known spawning site of the native trout population is indicated in Fig. 1. The spawning rubble, consisting of broken, mixed pieces (~ 10–30 cm length) of quartzite, feldspar, and granite, is underlain with solid bedrock. Water depth drops quickly to 8–10 m at ~ 5 m from the ~ 6-m^2 spawning site. No inlet streams are nearby. Drainage comes directly from a 10–30° sloping hillside consisting of undulating terrain covered with a heavy surface mat of ericaceous shrubs, mosses, and a tree cover dominated by *Pinus strobus*. The humus layer beneath this boreal forest is 3–25 cm thick. Midwinter frost penetration is ~ 30 cm. The glacial till soils consist of well-drained silt and sandy loams offering little or no acid-neutralizing capacity. Even the B-Bf horizons are very acidic (pH 3.9–4.7) and low in cation exchange capacity (3.3–12.0 meq/100 g).

Materials and Methods

Biological

During 1980 and 1981, extensive netting was used to locate spawning sites and assess the reproductive condition of the remaining lake trout. Up to seven trap nets and five gill nets were fished nightly for 10 d each year. In 1981, the spawning site rubble was searched for eggs by scuba divers. Eggs located at the end of the spawning period were reexamined in December to determine viability at the eyed stage. Three 0.36-m^2 emergent fry traps (Collins 1975) were set on the spawning bed 2 d after ice-out. The traps remained in place during May 8–21, 1982.

To assess possible natural recruitment, standard 72.6-m gill nets (2.5-, 3.8-, 5.1-, 6.4-, and 7.6-cm stretched-mesh mono-

filament) were fished during May, August, and October, 1982. In addition, six small mesh nets (1.3, 1.9, and 2.5 cm) were set during October 4–7, 1982.

For springtime bioassays, lake trout eggs were obtained from Tarentorous Hatchery on December 8, 1981. The eggs originated from Lake Manitou (pH 8.3, alkalinity > 2000 μeq/L) but were raised to the eyed stage in hatchery water (pH 6.9, alkalinity 400 μeq/L).

Five Plexiglas incubators (Kennedy 1980), each containing 50 eggs in separate chambers, were transferred to the lake on December 9, 1981. On February 22, 1982, shortly after the eggs had hatched, the incubators were moved to the experimental site (Fig. 2). The in situ bioassay began April 1, 1982, after the incubators were cleared of all dead eggs. The initial number of live sac fry at the start of the bioassay varied from 27 to 44 per incubator ($\bar{x} \pm SD = 37.1 \pm 7.2$). Inspections of the incubators began prior to significant snowmelt on April 2, 1982, and continued almost daily until May 10, 1982, 3 d after ice-out. Incubators were carefully lifted to the surface and remained submerged in a tray of lake water during mortality counts and removal of dead sac fry.

As controls, incubators were buried in perforated 10-L plastic pails filled with crushed limestone. Such substrates have previously been shown to maintain near-neutral interstitial pH and permit high survival of salmonids under acidic ambient conditions (Gunn and Keller 1980, 1981). A set of five pails, each with one incubator, was placed at 1 m depth approximately 30 m from the spawning site and an additional set of five pails was placed at a similar site on the south shore (Fig. 1). Control incubators were set out on December 9–10, 1981, and were inspected during February 22–23 and May 7–8, 1982.

To assess survival during the period of emergence and commencement of exogenous feeding, survivors from the spawning site incubators were transferred to 1-L plastic screened pens 3 d after ice-out. Twelve pens, each containing 10 alevins, were suspended at 0.5 m depth for a 10-d holding period. Lengths and dry weights were determined for subsamples of the alevins collected before and after the holding period.

Chemical and Physical

Water was sampled for pH, conductivity, dissolved oxygen, temperature, and concentrations of major ions and trace metals at the spawning site on six occasions between January 14 and March 30, 1982. Commencing on April 1, 1982, this site was sampled approximately weekly for major ions and trace metals and on a daily basis for the other parameters. In addition, 10 stations located at ~100-m intervals along the south and southeast sides of the lake (Fig. 1) were sampled on a daily basis for pH and conductivity to evaluate temporal and spatial variability in nearshore chemistry during snowmelt. All stations had depths (0.7–1.0 m) and substrates similar to the known spawning site.

An interstitial water sampler (Fig. 2) was installed to permit investigation of chemical conditions within the substrate. The depth at which the sampler was buried (~ 30 cm) corresponded to the approximate depth at which native eggs had been found. The apparatus consisted of a bottomless 250-mL Nalgene wash bottle equipped with a Plexiglas deflection plate and a 2-m length of 0.8-cm (i.d.) tygon tubing. All connections were sealed with clear silicone. Water was drawn through the attached tube with a peristaltic pump and samples were collected after a suitable flushing period determined from trial runs. Samples of ambient water at the spawning site were similarly collected with a peristaltic pump and tygon tubing at 15 cm above the substrate surface.

At other stations, water samples were taken using a 2 m × 3.5 cm (i.d.) Plexiglas tube. The tube, stoppered at both ends, was inserted vertically through an ice hole until it contacted the substrate. Removal of the upper stopper allowed water to enter through a 0.5-cm-diameter aperture located 15 cm from the bottom of the tube. The tube method allowed all stations to be quickly sampled at a standard distance above the substrate and eliminated the freezing problems associated with other mechanical sampling devices.

The daily samples for pH and conductivity were analyzed at the Whitepine Lake field station (Radiometer model 29 pH meter; YSI model 33 conductivity meter) within 12 h of collection. Weekly duplicates were analyzed at the Ontario Ministry of the Environment (MOE) laboratory in Sudbury to ensure the accuracy of field instruments. Samples for other chemical analyses were analyzed at the MOE laboratories in Toronto. Sample containerization, preservation, and analytical methods followed MOE (1981). Dissolved oxygen and temperature measurements were carried out in situ (YSI model 54 meter).

Commencing April 12, 1982, weekly samples of interstitial and ambient spawning site water were taken for Al fractionation studies. Samples were placed in 250-mL Nalgene bottles (acid washed and distilled–deionized and lakewater rinsed). Sealed dialysis bags (molecular weight cutoff 1000) filled with distilled–deionized water were incubated in the sample bottles for 12 h at 22°C. After incubation, inorganic (monomeric) Al was extracted from the contents of the dialysis bags by addition of an organic chelator (oxine) subsequently extracted into methyl isobutyl ketone (B. LaZerte, Water Resources Branch, Ontario Ministry of the Environment, pers. comm.). Aluminum analyses on extracts were conducted by graphite furnace atomic absorption spectroscopy. Concentrations of inorganic Al species, including Al^{3+} and hydroxide, fluoride, and sulphate complexes, were calculated from extracted inorganic Al concentrations, concentrations of other solutes, and thermodynamic constants (B. LaZerte, pers. comm.).

Air temperature (minimum, maximum), ice thickness, and occurrence of snow and rainfall were recorded daily commencing April 3, 1982. Rainfall for pH measurements was collected on an individual event basis in a 20-cm (i.d.) "Sangamo" precipitation sampler bucket lined with a clean plastic bag. A "drip" sampler consisting of a 10-L Nalgene pail was installed on April 16, 1982, at a site below an overhanging rock face near the spawning site to collect direct runoff. The pail was emptied and rinsed with distilled water daily. Volumes were recorded and samples were retained for chemical analyses. On seven occasions during various phases of snowmelt, replicate snow cores ($N = 4–6$) were collected from random locations in the forested area adjacent to the spawning site with a 12.1-cm (i.d.) Plexiglas tube. Water equivalents for each core were determined and samples were analyzed for selected chemical parameters.

Results

Snowpack, Runoff, and Rain Chemistry

The chemical composition of the snowpack adjacent to the spawning site showed considerable temporal variation. Average

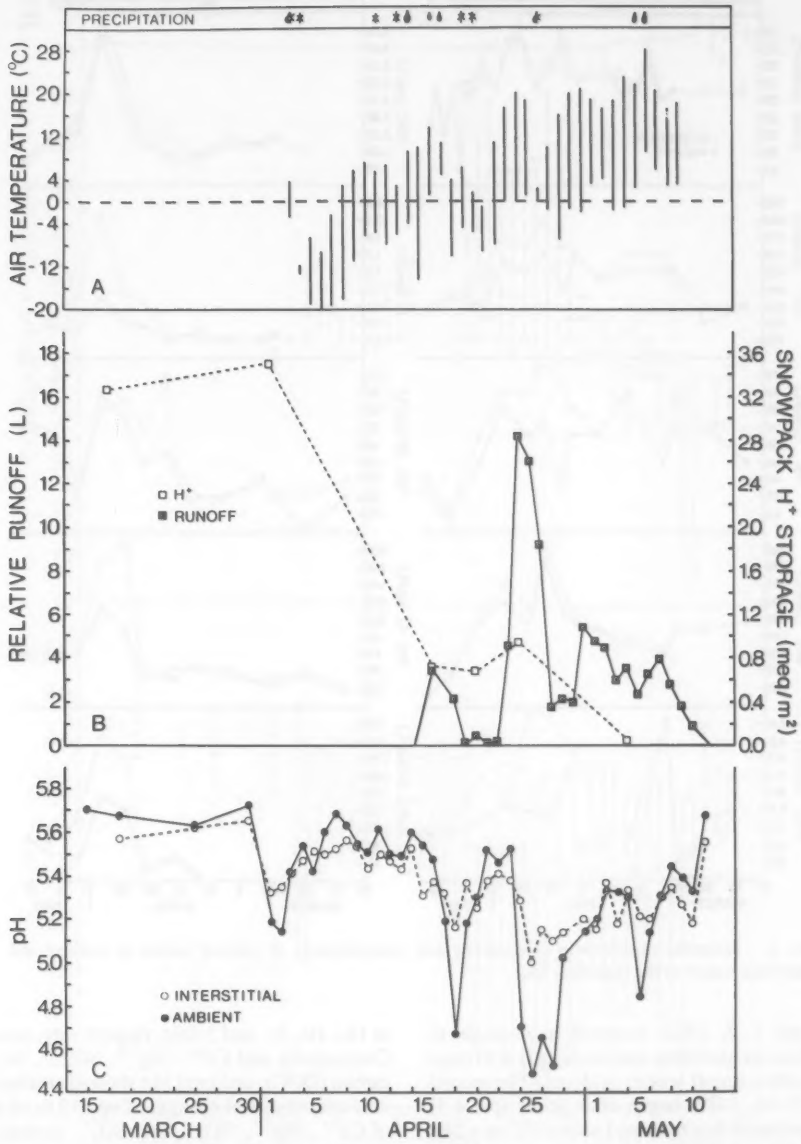


FIG. 3. Temporal variations in (A) air temperature, (B) snowpack H^+ storage and relative surface runoff volume, and (C) ambient and interstitial pH at the spawning site during the study period.

snowpack pH ranged from 4.5 to 5.2. Substantial depletion of H^+ (31–6 μeq/L), SO_4^{2-} (62–8 μeq/L), and NO_3^- (31–8 μeq/L) occurred in the snowpack through winter–spring. Concentrations of Ca^{2+} (5–40 μeq/L) and total Al (21–86 μg/L) in the snowpack increased with the onset of snowmelt and spring rains in mid-April, and then decreased in the last fraction of the snowpack. Concentrations of total Cu and Ni were low, generally < 3 and < 2 μg/L for Cu and Ni, respectively, with no temporal concentration pattern in evidence.

Runoff samples had low pH (3.9–4.3, $N = 25$), similar to the pH of soils measured in summer. Analyses of these samples collected on three occasions showed high color (71–89 Hazen units) and much higher concentrations of total Al (470–1500 μg/L) than snowpack samples.

Rainfall during the seven events was consistently acidic (pH 3.6–4.9). From measurements at Sudbury, spring rainfall during 1982 was low (24.5 mm during April) in comparison with long-term averages (~45 mm for April, Environment Canada 1982).

Nearshore Water Chemistry

The ambient waters at the spawning site exhibited four distinct episodes of substantial pH depression (Fig. 3C). The

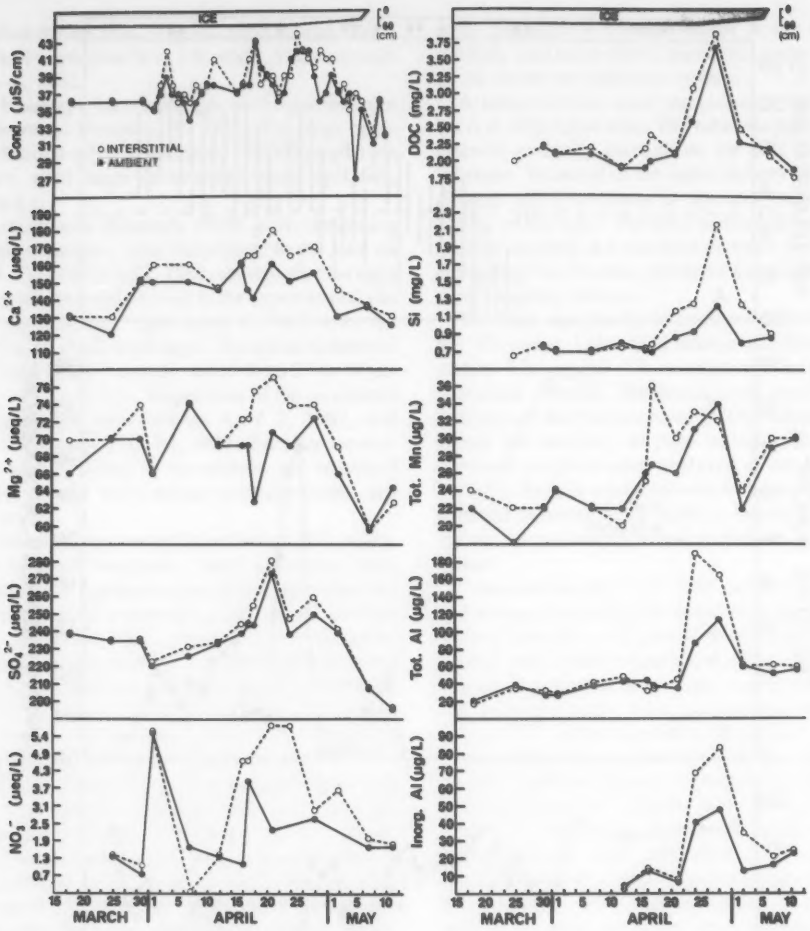


FIG. 4. Temporal variations in conductivity and concentrations of selected solutes in ambient and interstitial waters at the spawning site.

earliest episode (April 1–2, 1982) occurred in response to above-freezing daytime temperatures and acidic (pH 4.8) rains at a time when no surface runoff was in evidence. The second depression (April 17–19, 1982) began after acidic (pH 4.5) rains, when air temperatures first remained above 0°C on a 24 h basis (Fig. 3A) and substantial surface runoff commenced (Fig. 3B). With the return of subfreezing temperatures runoff subsided and ambient pH increased. The third depression (April 24–28, 1982), with the longest duration and lowest observed pH (4.5), coincided with the period of maximum runoff (Fig. 3B), stimulated by very warm daytime temperatures (Fig. 3A). Maximum surface runoff did not correspond with maximum snowpack H^+ depletion, which occurred previously (Fig. 3B). A last short (May 5, 1982), low pH event occurred shortly before ice breakup after heavy rains of very low pH (3.6). The first three periods of pH depression were associated with increases in the conductivity of nearshore water, while the last low pH episode was characterized by reduced conductivity (Fig. 4).

Concentrations of H^+, inorganic Al, NO_3^-, and total Al exhibited large temporal changes (Fig. 4), with variations of up to 15-, 10-, 8-, and 5-fold, respectively, over the study period. Conductivity and Ca^{2+}, Mg^{2+}, SO_4^{2-}, Si, dissolved organic carbon (DOC), and total Mn showed smaller temporal fluctuations with observed changes of up to 2 twofold. Concentrations of Ca^{2+}, Mg^{2+}, NO_3^-, and SO_4^{2-} peaked before maximum runoff, while H^+, DOC, Si, Mn, and Al peaked during or shortly after maximum runoff (Fig. 4). Total Cu and total Ni consistently approached detection limits (1 and 2 µg/L, respectively). Total Fe (10–45 µg/L) remained below the open-lake average (49 µg/L). Dissolved oxygen remained above 10 mg/L. Temperatures under ice were < 1.0°C during most of the study period. A gradual temperature increase (1.0–4.6°C) occurred during the last week preceding ice-out.

Fluoride complexes were the predominant form of inorganic Al (3.2–37.8 µg/L) in the ambient water, followed in importance by hydroxide complexes (1.0–12.4 µg/L) and Al^{3+} (0.2–5.9 µg/L). Sulphate complexes were present in very low concentrations (< 0.8 µg/L). Increases in all inorganic Al species occurred during maximum runoff.

Substantial differences in pH existed between the ambient and interstitial water at the spawning site (Fig. 3C). The pH

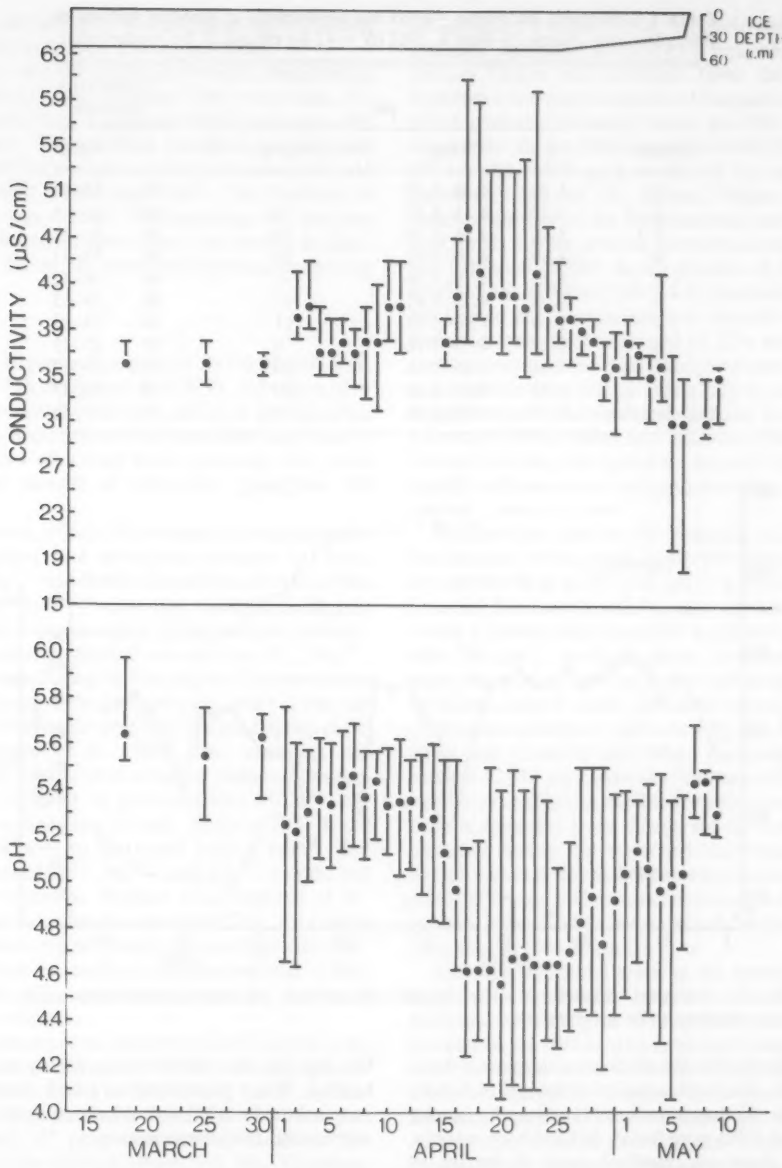


FIG. 5. Daily variations (mean and range) in pH and conductivity at 10 nearshore sampling sites.

within the substrate was often slightly lower than in the waters above, but pH within the substrate was consistently higher than in the ambient water during low pH episodes. The minimum pH recorded within the substrate was 5.0, while 15 cm above the substrate surface a minimum pH of 4.5 was recorded. Higher concentrations of Ca^{2+}, Mg^{2+}, SO_4^{2-}, NO_3^-, DOC, Si, total Mn, total Al, and inorganic Al occurred in interstitial samples, in comparison with ambient samples, at the spawning site (Fig. 4). At peak inorganic Al concentrations, hydroxide complexes were relatively more important in interstitial waters (22–42%) than in ambient waters (9–14%).

The pH and conductivity of shoreline waters showed considerable spatial variation (Fig. 5). Intersite differences were small prior to snowmelt, with maximum daily variation (up to 25-fold for H^+) occurring during the major runoff period. After ice breakup and commencement of spring turnover, shoreline stations again exhibited little between-site variation in these parameters.

Although changes in pH were not temporally synchronous among sites, all sites showed pH minima of ≤4.6. Sites with average pH < 5.0 were subjected to extended periods of low pH in comparison with other sites (Table 1).

Bioassays

The mean survival (± SD) of lake trout sac fry during the snowmelt bioassay was 81.8 ± 13.0%. Most mortalities

TABLE 1. Averages and ranges for pH and conductivity at shoreline stations on Whitepine Lake, March 18–May 9, 1982 (N = 42 for pH and 37 for conductivity).

Station	pH			Conductivity (μS/cm)	
	$\bar{x}$	Range	No. of days ph < 5.0	$\bar{x}$	Range
1	5.20	4.58–5.68	6	38	31–50
2	5.22	4.43–5.67	4	40	31–61
3	5.10	4.55–5.75	10	38	31–45
4	4.89	4.30–5.62	10	38	30–47
5	5.13	4.19–5.96	5	36	18–42
6	4.99	4.25–5.67	12	38	20–55
7	5.08	4.50–5.62	11	39	30–53
8	5.23	4.50–5.76	9	37	27–45
9	4.64	4.06–5.66	20	41	30–60
10	4.67	4.28–5.48	20	39	30–47
Spawning site	5.15	4.48–5.72	6	37	27–43

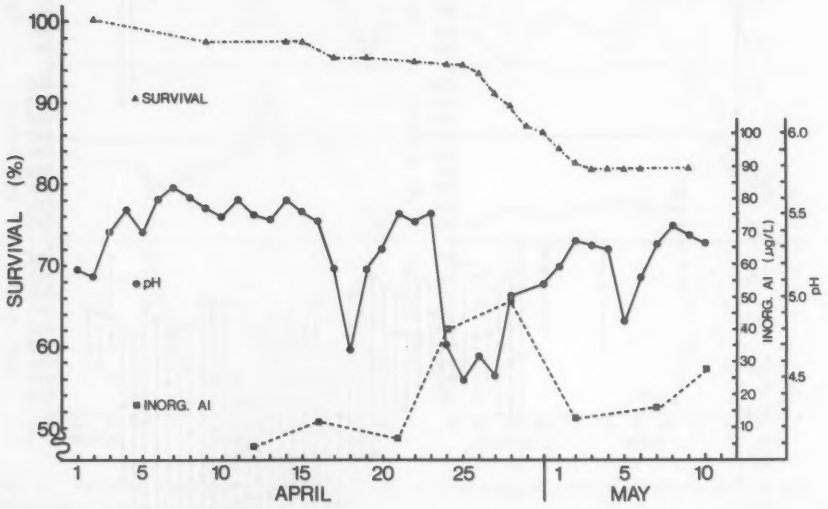


FIG. 6. Temporal variations in $\bar{x}$ sac fry survival, ambient pH, and inorganic (monomeric) Al concentrations at the spawning site.

occurred during or shortly after the pH depression event of April 24–28, 1982 (Fig. 6). During this period of low pH (4.5–5.0) and elevated inorganic Al concentrations (41–49 μg/L), sac fry were notably stressed. Gills were flared, fins and body margins were whitish, and observers classified most of the fry as moribund. However, the sac fry quickly recovered when runoff subsided and pH returned to > 5.0 and inorganic Al decreased to < 25 μg/L. No mortality occurred during the final days of the 37-d bioassay, which included the rapid retreat of the icepack from the shoreline and the complete disappearance of ice cover.

Very little mortality occurred in the control incubators. Survival in the south and southeast sets was 98.4 ± 1.7 and 97.1 ± 1.8%, respectively.

At ice-out, survivors from the spawning site incubators were similar to early emergent alevins (Gunn and Keller 1981) in yolk reserves (10–30%) and mobility. During the subsequent 10-d holding experiment only a single alevin (< 1%) died. Dry weight ($\bar{x}$ ± SD) decreased by 39.1% from 23.99 ± 4.76 to 14.61 ± 2.74 g and fork length (FL) increased from 2.28 ± 0.12 to 2.39 ± 0.08 cm as remaining yolk reserves were exhausted. On day 10, the alevins were highly mobile and appeared healthy. When transferred to a tank containing concentrated zooplankton from Whitepine Lake, they fed actively on *Cyclops scutifer* and *Diaptomus minutus*.

Native Lake Trout

The capture of reproductively spent native fish (3 female, 5 male) indicated that spawning occurred during the first 2 wk of October at 8–10°C. The presence of viable eggs within the rubble of the spawning site was confirmed by scuba divers on October 28, 1981. These eggs successfully reached the eyed stage, as indicated by the recovery of 20 viable eggs by divers on December 10, 1981. The eggs were relatively large (~ 6 mm in diameter) and brightly colored, thus appearing to be of good quality. Large numbers of dead fungus-covered eggs were also observed, but such observations are common even in highly productive lake trout lakes (Martin 1957).

No alevins were captured in the three emergent traps placed on the spawning site. The site rubble, however, had been

disturbed by divers, and alevins could also have easily avoided the traps by slight lateral motion into deeper water.

During the summer and fall netting assessment, five juvenile lake trout were captured: two yearlings (1981 year-class, FL 12.1 and 14.0 cm) and three fingerlings (1982 year-class, FL 7.7, 7.9, and 8.7 cm). The yearlings may have originated as escaped sac fry, of hatchery origin, used in preliminary survival studies during October 1980–May 1981. The number of potential escaped fry was < 1000. The fingerlings still had parr markings and were definitely native trout that existed as eggs, sac fry, and alevins during our period of chemical monitoring and in situ bioassays.

Discussion

In the last decade, Hagen and Langeland (1973), Haapla et al. (1975), Hultberg (1977), Jeffries et al. (1979), and others have documented pH depressions in streams and lakes during spring snowmelt. Our study demonstrated that nearshore lake waters, specifically the waters of a lake trout spawning site, were subjected to similar periods of substantial springtime pH depression.

In Norwegian streams, effects of snowmelt on water chemistry have been described as a three-phase process: (1) basic cations (Ca^{2+} and Mg^{2+}) are flushed from the soil water of the catchment at the beginning of snowmelt, resulting in slightly increased streamwater concentrations, (2) streamwater concentrations of atmospherically supplied ions such as H^+, SO_4^{2-}, and NO_3^- reach maxima during the first stages of snowmelt due to preferential ion release from the snowpack, and (3) ions are generally diluted by dilute meltwater from the last fraction of the snowpack (Johannessen et al. 1980). Our spawning site underwent a generally similar chronology of chemical changes (Fig. 4), including increases in concentrations of Ca^{2+} and Mg^{2+} near the commencement of melt, peaks in SO_4^{2-} and NO_3^- concentrations prior to maximum surface runoff, and reduced concentrations of Ca^{2+}, Mg^{2+}, and SO_4^{2-} near the end of runoff but prior to ice-out. Highest concentrations of H^+ coincided with the period of maximum runoff (Fig. 3), similar to observations in south-central Ontario streams (Jeffries et al. 1979) but differing from the results of Johannessen et al. (1980) who found that peak H^+ concentrations preceded maximum runoff in Norwegian streams.

The relative importance of soil–water reactions (Harvey et al. 1981) and ionic separation during snowmelt (Johannessen and Henriksen 1977; Colbeck 1981) in determining runoff chemistry cannot be fully evaluated with our data. However, the depletion of snowpack H^+ prior to observed runoff and the elevation of lithologically derived solutes (Al, Mn, Si) during the major pH depression period indicate the importance of reactions in the soil–litter layer during snowmelt to shoreline chemistry. We observed little direct surface flow during snowmelt, and the physiography of the site and the chemical composition of the runoff water suggested that considerable downward flow and lateral displacement of soil water occurred. The relative contribution of seepage and surface water flow during runoff is highly variable, temporally and spatially (Holecek and Noujaim 1972; Seip 1980; Beven and Germann 1982); thus, our shoreline sites could display considerable annual chemical variability based on physical characteristics of the melt.

The observed increase in concentrations of inorganic Al during the major runoff period is biologically important, since Al appears to cause fish mortalities under acidic conditions (Muniz and Leivestad 1980a; Schofield and Trojnar 1980). The inorganic portion of the total Al is recognized as the most toxic fraction (Baker and Schofield 1980; Driscoll et al. 1980). Reported toxic concentrations of inorganic Al for salmonids in dilute synthetic laboratory water are 500 μg/L at pH 5.2 for brook trout alevins (Baker and Schofield 1980), > 100 μg/L at pH 4.5 and > 500 μg/L at pH 5.5 for rainbow trout (*Salmo gairdnerii*) sac fry (K. Holtze, Water Resources Branch, Ontario Ministry of the Environment, pers. comm.), and 200 μg/L at pH 5.0 for juvenile brown trout (*Salmo trutta*) (Muniz and Leivestad 1980b). In the absence of Al, the various trout species were tolerant of pH < 4.5. However, the laboratory data are limited and extrapolations to natural waters are difficult. Reported toxic thresholds and LC50's are based on nominal concentrations. Marked declines in Al concentrations in the test tanks, presumably through precipitation, have been noted in the supersaturated solutions used in these bioassays (Muniz and Leivestad 1980b; Baker and Schofield 1982; K. Holtze, pers. comm.). Further, the reported inorganic Al concentrations may include polymeric and colloidal forms as well as monomeric species.

No laboratory data on pH–inorganic Al interactions exist in the literature for lake trout. Under pH stress alone, lake trout sac fry exhibit 96-h LC50's of pH < 4.0 (W. Kwain, Fisheries Research Section, Ontario Ministry of Natural Resources, pers. comm.). During field exposures to pH 4.6 and total Al levels of 400–700 μg/L, in clear, dilute (conductivity ~ 35 μS/cm) water, the median survival time of lake trout alevins was 40 h (J. M. Gunn, unpubl. data). Our observation that despite previous short-term exposures to pH near 5.0, lake trout sac fry suffered stress and mortality only when inorganic Al concentrations reached 41–49 μg/L provides further evidence that Al toxicity may be primarily responsible for fish mortalities during acidification episodes. Even though sac fry experienced stress and mortality during the major pH depression period, the high overall survival (82%) indicates that under natural conditions most sac fry can endure short-term (up to at least 5 d) exposure to low pH (< 5.0) and relatively high concentrations of inorganic Al (40–50 μg/L).

Although interstitial water at the spawning site maintained higher pH (≥ 5.0) than ambient water (≥ 4.5), the fact that inorganic Al was higher in interstitial waters (Fig. 6) indicates that natural sac fry could be subjected to more toxic effects than sac fry exposed in our incubators, particularly since the toxic effects of inorganic Al appear to be greatest at pH near 5.0. Baker and Schofield (1982) indicated that, in general, inorganic Al was most toxic in oversaturated solutions at pH 5.2–5.4. Schofield and Trojnar (1980) noted increasing Al toxicity in brook trout with increasing pH (4.4–5.2) at total Al concentrations of 0–1000 μg/L. Toxicity mechanisms under these conditions involved precipitation and coagulation of aluminum hydroxide on gill or other surfaces (Baker 1982). During the major pH depression event in Whitepine Lake, the proportion of inorganic Al contributed by the hydroxide complexes was greater in interstitial waters (22–42%) than in the lower pH ambient waters (9–14%).

Other researchers have also noted that interstitial chemistry differs from ambient conditions (Williams and Hynes 1974; Lacroix 1980). In Atlantic salmon (*Salmo salar*) redds, Lacroix (1980) found decreases in interstitial pH and dissolved oxygen during rising water temperatures in spring. Peterson et al. (1982) indicated that low alkalinity interstitial waters become more acidic under the influence of CO_2 release by the

decomposition of organic matter and respiration of streambed organisms. Interstitial CO_2 has been shown to increase as pH decreased with depth in a stream gravel bed (Williams and Hynes 1974). During our experiment, temperature and dissolved oxygen remained relatively constant under ice cover, the rubble was relatively clear of organic matter, and interstitial pH was elevated, not reduced, in relation to ambient conditions during pH depressions, suggesting that CO_2 production had little effect on fry survival. However, the role of free CO_2 in observed toxicities is uncertain.

Our observations on chemical changes and sac fry survival do little to explain the demise of the native lake trout population in Whitepine Lake. The successful spawning of native adults, the development of native eggs to the eyed stage, and the high survival of introduced yearlings suggest that past recruitment failures occurred at the sac fry to alevin stages. However, the high overall survival of sac fry and alevins during incubations and the collection of native fingerlings indicate that lake trout recruitment was possible and did occur during the spring of 1982. Our findings are very similar to those of Mills (1982) for artificially acidified Lake 223 in the Experimental Lakes Area. Lake trout continued to spawn but failed to recruit when the pH of Lake 223 was reduced to 5.4. Similar bioassays within the water column revealed little mortality of eggs and sac fry. Observed differences between interstitial and ambient chemistry may partially explain such discrepancies; however, other factors may be involved in Whitepine Lake. The spring of 1982 had comparatively little rain, with a total April rainfall of only 54% of the long-term average for the month (Environment Canada 1982). When snowmelt is augmented by heavy rains, more severe shoreline effects may occur. Additionally, general water quality improvements may be occurring in Whitepine Lake as a result of reduced emissions from the Sudbury smelting industry during the last decade (Anonymous 1982). Historical water quality data are not available for Whitepine Lake, but recent pH increases have been observed in some other Sudbury area lakes. Laundrie Lake, 15 km south of Whitepine Lake, exhibited a consistently lower pH (4.7–5.1 $N = 17$) during 1975–76 than during 1981–82 (5.2–5.4, $N = 11$) (W. Keller, unpubl. data).

The very short (~ 1–5 d) duration of low pH episodes and the large temporal and spatial variability in pH between nearshore sites illustrate the difficulty of evaluating spring melt effects on lake shoreline waters. The additional complication of substantial differences in chemistry between interstitial and ambient waters indicates that chemistry and fish effects occurring within the substrate may not be well described by conventional open-water sampling programs and field bioassays. Our findings of potentially more toxic chemical conditions in interstitial water may be the key to explaining differences between laboratory bioassay results and observed responses of natural populations to acidification.

Acknowledgments

We thank P. Gale and V. Liimatainen for participation in all aspects of the study, G. Bales and H. Eakins for field assistance, J. Casselman for age assessment of native trout, M. Kurshaw for characterization of soils and vegetation in the Whitepine Lake watershed, C. Lauer and J. Munro for transferring Al samples to Dorset, and G. Gorgichuk for many safe helicopter flights. Staff of the Laboratory Services Branch, MOE, performed the numerous laboratory analyses. C. Calvert, S. Langin, and V. Lee typed and corrected the manuscript. Special thanks are given to B. LaZerte for Al extractions and speciation and review of the manuscript. P. Dillon, J. MacLean, N. Yan, and two anonymous referees provided helpful comments on an earlier draft of this paper. This project was supported in part through funds provided by the Acidic Precipitation in Ontario Study (APIOS), a cooperative program of the Ontario Ministries of the Environment and Natural Resources.

References

ANONYMOUS. 1982. Report of the Ontario/Canada task force for the development and evaluation of air pollution abatement options for Inco Limited and Falconbridge Nickel Mines, Limited in the Regional Municipality of Sudbury, Ontario. Intergovernmental Task Force Report, Toronto, Ont. 255 p.

BAKER, J. P. 1982. Effects on fish of metals associated with acidification, p. 165–176. *In* Acid rain/fisheries. Proc. Int. Symp. Acidic Precip. Fish. Impacts Northeastern North America, Cornell University, Ithaca, NY.

BAKER, J. P., AND C. L. SCHOFIELD. 1980. Aluminum toxicity to fish as related to acid precipitation and Adirondack surface water quality, p. 292–293. *In* D. Drablos and A. Tollan [ed.] Ecological impact of acid precipitation. Proc. Int. Conf. Ecol. Impact Acid Precip., Sandefjord, Norway.

1982. Aluminum toxicity to fish in acidic waters. Water Air Soil Pollut. 18: 289–309.

BEAMISH, R. J., AND H. H. HARVEY. 1972. Acidification of the La Cloche Mountain lakes, Ontario, and resulting fish mortalities. J. Fish. Res. Board Can. 29: 1131–1143.

BEAMISH, R. J., W. L. LOCKHART, J. C. VAN LOON, AND H. H. HARVEY. 1975. Long-term acidification of a lake and resulting effects on fishes. Ambio 4: 98–102.

BEVEN, K., AND P. GERMANN. 1982. Macropores and water flow in soils. Wat. Resour. Res. 18: 1311–1325.

COLBECK, S. C. 1981. A simulation of the enrichment of atmospheric pollutants in snow cover runoff. Wat. Resour. Res. 17: 1383–1388.

COLLINS, J. J. 1975. An emergent fry trap for lake spawning salmonines and coregonines. Prog. Fish Cult. 37: 140–142.

DILLON, P. J., D. S. JEFFRIES, W. A. SCHEIDER, AND N. D. YAN. 1980. Some aspects of acidification in southern Ontario, p. 212–213. *In* D. Drablos and A. Tollan [ed.] Ecological impact of acid precipitation. Proc. Int. Conf. Ecol. Impact Acid Precip., Sandefjord, Norway.

DILLON, P. J., D. S. JEFFRIES, W. SNYDER, R. REID, N. D. YAN, D. EVANS, J. MOSS, AND W. A. SCHEIDER. 1978. Acidic precipitation in south-central Ontario: recent observations. J. Fish. Res. Board Can. 35: 809–815.

DRISCOLL, C. T., J. P. BAKER, J. J. BISOGNI, AND C. L. SCHOFIELD. 1980. Effect of aluminum speciation on fish in dilute acidified waters. Nature (London) 284: 161–164.

ENVIRONMENT CANADA. 1982. Monthly records — meteorological observations in eastern Canada. Vol. 67. No. 4. Atmospheric Environment Service, Downsview, Ont.

GUNN, J. M. 1982. Acidification of lake trout (*Salvelinus namaycush*) lakes near Sudbury, Ontario, p. 351. *In* Acid rain/fisheries. Proc. Int. Symp. Acidic Precip. Fish. Impacts northeastern North America, Cornell University, Ithaca, NY.

GUNN, J. M., AND W. KELLER. 1980. Enhancement of the survival of rainbow trout (*Salmo gairdneri*) eggs and fry in an acid lake through incubation in limestone. Can. J. Fish. Aquat. Sci. 37: 1522–1530.

1981. Emergence and survival of lake trout (*Salvelinus namaycush*) and brook trout (*S. fontinalis*) from artificial substrates in an acid lake. Ont. Fish. Tech. Rep. Ser. No. 1: 9 p.

HAAPLA, H., P. SEPPONEN, AND E. MESKUS. 1975. Effects of spring floods on water acidity in the Kiiminkijoki area, Finland. Oikos 26: 26–31.

HAGEN, A., AND A. LANGELAND. 1973. Polluted snow in southern Norway and the effect of the meltwater on freshwater aquatic organisms. Environ. Pollut. 5: 45–57.

HAINES, T. A. 1981. Acidic precipitation and its consequences for aquatic ecosystems: a review. Trans. Am. Fish. Soc. 110: 669–707.

HARVEY, H. H., R. C. PIERCE, P. J. DILLON, J. R. KRAMER, AND D. M. WHELPDALE. 1981. Acidification in the Canadian aquatic environment. Publication NRCC No. 18475. Environmental Secretariat, National Research Council of Canada, Ottawa, Ont. 369 p.

HOLECEK, G. R., AND A. A. NOUJAIM. 1972. Separation of the surface and subsurface flow from snowmelt by the use of radioactive tracers. Proc. Western Snow Conference, 40th Annu. Meet., Fort Collins, CO.

HULTBERG, H. 1977. Thermally stratified acid water in the late winter – a key

factor inducing self-accelerating processes which increase acidification. Water Air Soil Pollut. 7: 279–294.

JEFFRIES, D. S., C. M. COX, AND P. J. DILLON. 1979. Depression of pH in lakes and streams in central Ontario during snowmelt. J. Fish. Res. Board Can. 36: 640–646.

JOHANNESSEN, M., AND A. HENRIKSEN. 1977. Chemistry of snowmelt water: changes in concentration during melting. SNSF Tech. Rep. FR11/77. Oslo, Norway. 11 p.

JOHANNESSEN, M., A. SKARTVEIT, AND R. F. WRIGHT. 1980. Streamwater chemistry before, during and after snowmelt, p. 224–225. *In* D. Drablos and A. Tollan [ed.] Ecological impacts of acid precipitation. Proc. Int. Conf. Ecol. Impact Acid Precip., Sandefjord, Norway.

JOHNSON, N. M. 1979. Acid rain: neutralization within the Hubbard Brook ecosystem and regional implications. Science (Washington, DC) 204: 497–499.

KELLER, W., J. M. GUNN, AND N. I. CONROY. 1980. Acidifiction impacts on lakes in the Sudbury, Ontario, Canada area, p. 228–229. *In* D. Drablos and A. Tollan [ed.] Ecological impacts of acid precipitation. Proc. Int. Conf. Ecol. Impacts Acid Precip., Sandefjord, Norway.

KELSO, J. R. M., AND J. M. GUNN. 1982. Responses of fish communities to acidic waters in Ontario. *In* G. R. Hendrey [ed.] Chronic stress of acidification on aquatic biota: pH 5 to 6. Am. Chem. Soc. Symp. Ser., Ann Arbor Science Publishers, Ann Arbor, MI.

KENNEDY, L. A. 1980. Teratogenesis in lake trout (*Salvelinus namaycush*) in an experimentally acidified lake. Can. J. Fish. Aquat. Sci. 37: 2355–2358.

LACROIX, G. L. 1980. The reproductive environment of land-locked Atlantic salmon (*Salmo salar* L.). Ph.D. thesis. University of New Brunswick, Fredricton, N.B. 326 p.

MARTIN, N. V. 1957. Reproduction of lake trout in Algonquin Park, Ontario. Trans. Am. Fish. Soc. 86: 231–244.

MARTIN, N. V., AND C. H. OLVER. 1976. The distribution and characteristics of Ontario lake trout lakes. Ont. Min. Nat. Res. Fish. Wild. Res. Branch Rep. 97: 30 p.

MILLS, K. H. 1982. Fish population responses during the experimental acidification of a small lake. *In* G. R. Hendrey [ed.] Chronic stress of acidification on freshwater biota: pH 5 to 6. Am. Chem. Soc. Symp. Ser., Ann Arbor Science Publishers, Ann Arbor, MI.

MINISTRY OF THE ENVIRONMENT (MOE). 1981. Outlines of analytical methods. MOE Tech. Rep., Toronto, Ont. 246 p. plus appendix.

MUNIZ, I. P., AND H. LEIVESTAD. 1980a. Acidification-effects on freshwater fish, p. 84–92. *In* D. Drablos and A. Tollan [ed.] Ecological impact of acid precipitation. Proc. Int. Conf. Ecol. Impact Acid Precip., Sandefjord, Norway.

1980b. Toxic effects of aluminum on the brown trout, *Salmo trutta* L., p. 320–321. *In* D. Drablos and A. Tollan [ed.] Ecological impacts of acid precipitation. Proc. Int. Conf. Ecol. Impact Acid Precip., Sandefjord, Norway.

PETERSON, R. H., P. G. DAYE, G. L. LACROIX, AND E. T. GARSIDE. 1982. Reproduction in fish experiencing acid and metal stress, p. 177–196. *In* Acid rain/fisheries. Proc. Int. Symp. Acidic Precip. Fish. Impacts Northeastern North America, Cornell University, Ithaca, NY.

SCHEIDER, W. A., D. S. JEFFRIES, AND P. J. DILLON. 1979. Effects of acidic precipitation on precambrian freshwaters in southern Ontario. J. Great Lakes Res. 5: 45–51.

SCHINDLER, D. W., R. H. HESSLEIN, R. WAGEMANN, AND W. S. BROECKER. 1980. Effects of acidification on mobilization of heavy metals and radionuclides from the sediments of a freshwater lake. Can. J. Fish. Aquat. Sci. 37: 373–377.

SCHOFIELD, C. L. 1976. Acid precipitation: effects on fish. Ambio 5: 228–230.

SCHOFIELD, C. L., AND J. R. TROJNAR. 1980. Aluminum toxicity to brook trout (*Salvelinus fontinalis*) in acidified waters, p. 341–366. *In* T. Y. Toribara, M. W. Miller, and P. E. Morrow [ed.] Polluted rain. Plenum Press, New York, NY.

SEIP, H. M. 1980. Acidification of freshwater — sources and mechanisms, p. 358–366. *In* D. Drablos and A. Tollan [ed.] Ecological impact of acid precipitation. Proc. Int. Conf. Ecol. Impact Acid Precip., Sandefjord, Norway.

WILLIAMS, D. D., AND H. B. N. HYNES. 1974. The occurrence of benthos deep in the substratum of a stream. Freshw. Biol. 4: 233–256.

Divergent Structure in Fish Taxocenes of North Temperate Streams

Robin Mahon[1]

Zoology Department, University of Guelph, Guelph, Ont. N1G 2W1

Mahon, R. 1984. Divergent structure in fish taxocenes of north temperate streams. Can. J. Fish. Aquat. Sci. 41: 330–350.

The fish taxocenes of two typical river systems in Poland and Ontario differed in patterns of species richness, distribution, life history, and ecomorphology. In small streams there were more small nektonic and benthic fishes in Ontario. In Poland where large, nektonic cyprinids dominate, the fishes were larger, longer lived, later maturing, and absolutely and relatively more fecund and had longer reproductive spans, but egg diameters were similar. In Ontario, nester/guarders and brood hiders were common, whereas in Poland all but three species broadcast eggs. Small-stream fishes were small, early maturing, short lived, and sedentary and gave parental care to few, large eggs. Large-river fishes displayed opposite characteristics and often migrated to spawn in habitats suitable for young but not adults. The factor space of a principal components analysis of ecomorphological characteristics corresponded roughly to a longitudinal gradient in fluvial conditions. There was a significantly higher proportion of fishes from Poland in the downstream half of the space, and vice versa. The most prominent differences in taxocene structure generalize to west-central Europe and east-central North America. Evidently, several groups of North American fishes invaded and became adapted to small streams, facilitating speciation. European fishes retained the strategy of seasonal/ontogenetic longitudinal migration. Ancestors to the most diverse groups in North America inhabited both continents; consequently, long-term climatic patterns (glaciation) and/or the influence of lowland ichthyofauna are the most likely causes of the differences.

Les taxocènes ichtyologiques de deux réseaux fluviaux typiques, l'un de Pologne et l'autre de l'Ontario, diffèrent quant au nombre d'espèces, leur distribution, cycle de vie et écomorphologie. Dans les petits cours d'eau, il y plus de petits poissons nectoniques et benthiques en Ontario. En Pologne, par ailleurs, là où dominent les grands cyprinidés nectoniques, les poissons sont plus gros, ont une plus longue durée de vie, atteignant la maturité à un âge plus avancé, sont plus féconds tant en termes absolus que relatifs et ont une durée de vie reproductrice plus longue, mais ont des œufs de diamètres identiques. En Ontario, les espèces qui défendent leur nid et cachent leur progéniture sont communs, alors qu'en Pologne, toutes les espèces, sauf trois, abandonnent leurs œufs. Les poissons des petits cours d'eau sont petits, ont une maturité hâtive, une courte durée de vie, sont sédentaires, et les parents veillent sur des œufs peu nombreux et gros. Les poissons des grands cours d'eau montrent des caractéristiques opposées et émigrent souvent pour frayer dans des habitats qui conviennent aux jeunes mais non aux adultes. Le facteur espace dans une analyse en composantes principales des caractéristiques écomorphologiques correspond à peu près à un gradient longitudinal des conditions fluviales. Il y a une proportion significativement plus forte de poissons en Pologne dans la moitié d'aval de l'espace et vice versa. Les différences les plus évidentes de structure de taxocène s'appliquent en général au centre-ouest d'Europe et le centre-est de l'Amérique du Nord. Il est évident que plusieurs groupes de poissons nord-américains ont envahi les petits cours d'eau et s'y sont adaptés, ce qui a facilité la spéciation. Les poissons européens ont conservé la stratégie d'une migration longitudinale saisonnière/ontogénique. Les ancêtres des groupes les plus diversifiés de l'Amérique du Nord ont habité les deux continents ; par conséquent, les caractéristiques climatiques à long terme (glaciation) et (ou) l'influence de l'ichtyofaune des terres basses sont les causes les plus probables des différences.

Received May 26, 1983
Accepted November 8, 1983

Reçu le 26 mai 1983
Accepté le 8 novembre 1983

Fluvial systems in general and small streams in particular are characterized by physical conditions that would be expected to profoundly influence the characteristics of the fishes that live there (Hubbs 1941). Given the stringency of the fluvial environment, it seems reasonable to hypothesize that fishes occupying physically similar streams in different parts of the world would evolve similar adaptations for stream life and that furthermore, these fishes would be assembled into taxocenes of similar structure. In this study, I make a first attempt to evaluate this hypothesis by comparing the fish taxocenes of two similar drainage basins, one in Poland the other in Ontario.

Several "convergence" studies, dealing almost exclusively with terrestrial ecosystems, have begun with similar hypotheses (Cody and Mooney 1978). Cody and Mooney (1978) listed conditions that would constrain the likelihood of finding convergent structure. They pointed out that the selective fields must be similar; that the organisms must be "... capable of producing and exposing to selection the appropriate phenotypes; that there must have been sufficient time for selection to have acted; and that there must be no confusing historical or chance events." Obviously, in any field study, most or all of these assumptions will be violated, and the extent to which this

[1]Present address: Marine Fish Division, Bedford Institute of Oceanography, Dartmouth, N.S. B2Y 4A2.

has occurred must be considered when drawing conclusions about the degree of taxocene convergence.

Typically, streams in mesic regions of Europe and North America provide a distinct gradient of habitats, ranging from physically demanding headwaters to nearly lacustrine lowland reaches (Vannote et al. 1980). Consequently, within climatically similar portions of the continents, convergence of fish taxocenes in streams of similar size and geomorphological configuration might be expected, especially as the freshwater fish faunas share many common ancestors owing to exchanges between the continents during the Mesozoic (Patterson 1981).

On the other hand, Europe and North America differ considerably topographically and with regard to the effects of glaciation on their fish faunas. North American freshwaters are dominated by the huge Mississippi drainage system, which acted as a refugium and a north–south corridor for fishes during glacial advances and retreats (Pfleiger 1971; Bailey and Smith 1981). In Europe, north–south movement of fishes was hindered by east–west mountain ranges, seas, and to the southeast, desert. Recolonization of northwestern Europe by fishes was circuitous via the east central lowland rivers draining into the Black and Caspian seas (Berg 1965; Banarescu 1975).

Patterns of species richness and distribution, life history, and ecomorphology will be compared between the taxocenes of the river systems. These aspects relate to three levels of biological organization, the taxocene, the population, and the individual, which are seldom considered together (Regier 1979). Each aspect has its own conceptual background, which will be briefly introduced.

In general, stream fish species richness has been found to increase in a downstream direction. This appears to be due partly to an increase in habitat diversity with stream size (Gorman and Karr 1978) and partly to decreasing abiotic variability (Horwitz 1978). Habitat diversity was viewed in terms of depth, current, and substrate, and abiotic variability was viewed in terms of discharge fluctuations that were found to be related to most physical parameters in fluvial systems. Horwitz (1978) compared the number of species accumulated along the length of the stream with the number found at any point in the stream. The diversity patterns of the fishes in the selected drainages in Poland and Ontario will be compared on the basis of similar curves.

Although recent reviews for coral reef (Barlow 1981) and desert fishes (Constantz 1981) have underscored the importance of dispersal and migration, there are very few interspecific comparisons of life history patterns in fishes. In this study I compare the life history parameters of fishes in the two taxocenes with reference to the "accepted scheme" (Stearns 1977), according to which certain traits commonly occur together, e.g. long life, late maturity, large size, iteroparity, small clutch size, and low reproductive effort. There are two hypotheses, both plausible, explaining how this combination might arise. The most cited is the concept of *r*- and *K*-selection (Pianka 1970), which predicts that the above combination will predominate in stable environments where populations are limited in a density-dependent fashion. An alternative hypothesis (Murphy 1968) predicts that the combination will predominate when unpredictable mortality affects juveniles more strongly than adults (see reviews by Stearns 1976; Law 1979). Explanations for combinations of characteristics that do not fit the "accepted scheme" are generally lacking (Stearns 1977). However, as there are many close associations among life history parameters in fishes (Svardson 1949; Beverton and Holt 1959; Blueweiss et al. 1978; Roff 1981), any constraint on one of these parameters is also likely to constrain associated traits (Stearns 1980).

The ability to adequately describe a species "niche" from its morphology would greatly aid comparison of species or assemblages (Hespenheide 1973). This would be particularly true for fishes, as they are difficult to observe in the field. Observations on the relatedness of form and function in fishes abound. These are reviewed by Gatz (1979), who considered the ecological significance of 54 attributes and examined the correlations among them for 28 species of stream fishes. Relatively few of the characteristics that he studied could be unambiguously related to a particular mode of life. This is probably because a given attribute may serve more than one function and also because there are often several ways in which different species may cope with the same environmental problem (Bock 1977).

Despite the apparent absence of a consistent relationship between ecology and morphology, Gatz's (1979) study does support the validity of several of the more widely accepted associations of body and fin form with mode of life. These relate primarily to the water velocity in which the fish lives, whether it swims actively or is sedentary, and whether it is benthic or nektonic. Therefore, in this study I compare the assemblages of fishes from the Grand and Nida rivers using principal component analysis (PCA) to ordinate the species on the basis of several ecomorphological characteristics known to reflect fluvial habitat use by fishes.

Drainage Basins

The Nida River, in south-central Poland, and the Grand River, in southern Ontario, are tributaries of the Vistula River and Lake Erie, respectively (Fig. 1). Based on the following comparison I believe that the systems are sufficiently similar to allow valid comparison of their fish taxocenes.

The climates of south-central Poland and southern Ontario are similar in many respects. Seasonal means and ranges in temperatures of Kielce (50°51′N, Okolowicz 1977) and Toronto (43°40′N, Hare and Hay 1974) are shown in Fig. 2. Although Kielce lies farther north than Toronto, winter temperatures are no lower. Summer is a few degrees cooler due to the influence of the Baltic Sea. The curves (Fig. 2) indicate similar durations of summer and winter and similar diel temperature variations for both places. Mean annual precipitation at Toronto (Hare and Hay 1974) and Kielce (Okolowicz 1977) was 776 and 644 mm, respectively, for the 1931–60 period.

Discharge is probably the most important factor affecting fishes in fluvial systems (Horwitz 1978). There are two aspects to discharge: the seasonal pattern and the short-term response of the system to isolated, unpredictable rainfall events. Seasonal river regime is determined primarily by climate and drainage basin morphology (Beckinsale 1969), and the latter is, to some extent, influenced by the former (Gregory 1976). A classification of river regimes for the world indicates a large spring thaw peak for both regions (Beckinsale 1969). In Ontario, there is a secondary maximum in late fall. In Poland, no secondary peak is shown by Beckinsale (1969) but hydrographs for the Skawa and Raba rivers (Punzet 1969, 1976), Vistula tributaries about 100 km south of the Nida, show one in July when there is a rainfall maximum. There are two discharge peaks in the Nida River, with the spring one being the largest (Pasternak and

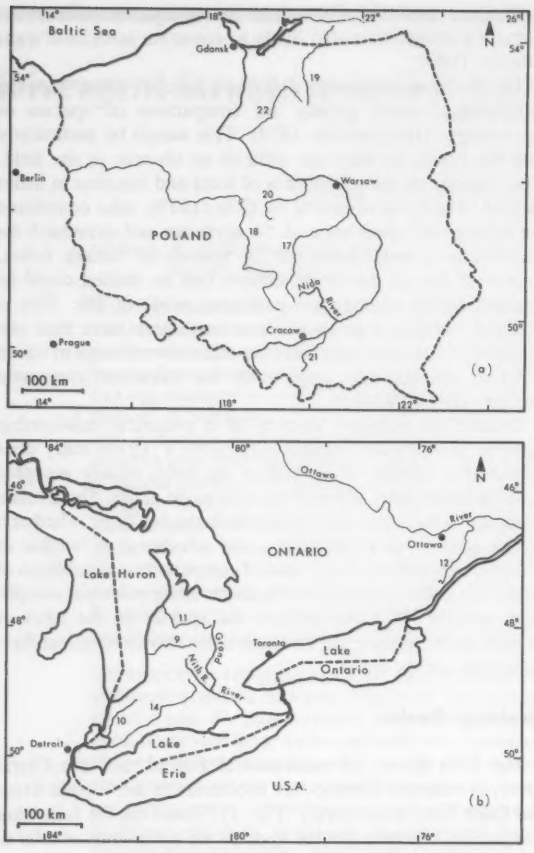


FIG. 1. Poland and southern Ontario showing the location of the Grand, Nida, and other rivers used in Table 1 (numbered as in Fig. 4).

Starjecka 1979). Hydrographs confirm the secondary peak in southern Ontario in October–November (Browzin 1962). The possible effects of the difference in the timing of the secondary peak are unknown.

Rivers in which there is a sharp flood peak would be less hospitable to fishes and their food organisms than those in which the peak is flatter (Horwitz 1978). A complex array of factors affect the flood peak (Rodda 1969). Transient characteristics such as storm behavior are important, but drainage basin morphology is more easily measured and has been most studied as a predictor of flood intensity. Most aspects of drainage basin morphology have been found to influence the flood peak. However, the important features vary among geographic regions and stream types (Patton and Baker 1976; Gurnell 1978). It seems possible to say only that the more morphologically similar two basins are, the more likely they will respond in similar ways to storms. As maps of similar scale were not available for both drainage areas, comparison of the Grand and Nida drainages is based on length, area, and gradient.

Both basins are at similar altitudes with similar ranges in elevation. Penczak (1971) provided the length, drainage area, and gradient for the Nida River and 21 of its tributaries. Among the tributaries the highest source is about 400 m above sea level (asl). The Nida enters the Vistula at 165 m asl. I consider the Grand River only above its confluence with the Nith River (Fig.

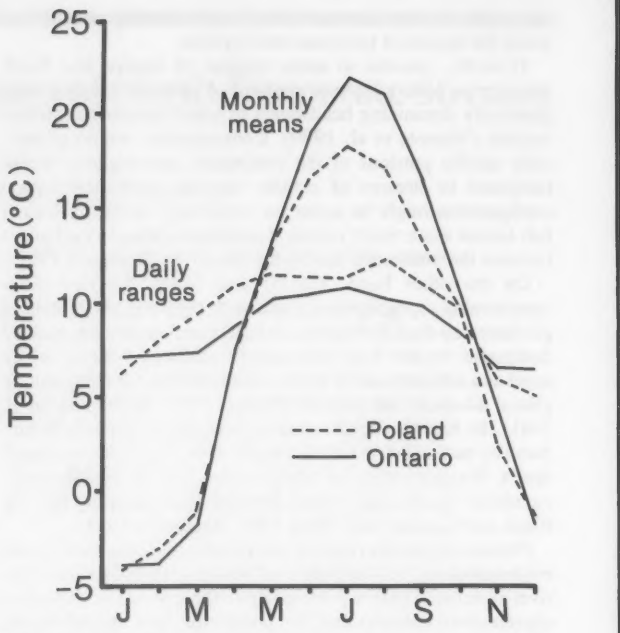


FIG. 2. Mean monthly air temperature and mean daily range are similar for Kielce, Poland, and Toronto, Ont. (1931–60).

1). For the main channel, and for 21 tributaries for which information on fish distribution was available, I estimated channel length, drainage area, and gradient from 1 : 50 000 topographic maps. Among these tributaries the maximum elevation of a source is 450 m asl; the confluence of the Grand and Nith rivers is at 230 m asl.

The relationships between the log of main channel length and the log of area for the drainage basins were significant for both river systems, and neither the slopes nor the intercepts differed significantly between them (Fig. 3a). This indicates that the river systems are similar in shape. Similarly, the relationships between basin area and gradient were significant for both systems but did not differ significantly between them (Fig. 3b). Thus, basins of similar size in both systems have similar relief and, consequently, similar levels of productivity (Cushing et al. 1980).

Given the similarity in latitudes of the two systems, they would have similar net amounts and seasonal patterns of solar radiation. Percentage cloudiness is 62% in Toronto (Hare and Hay 1974) and 66% in Kielce (Okolowicz 1977), for example. The drainages are also similar in terms of nutrient loading as estimated by conductivity. The means and ranges of conductivity (siemens per centimetre) measured monthly at six localities in each system during 1978–79 were 438 (322–480) and 396 (245–600) for the Nida and Grand rivers, respectively.

Methods

Fish Distribution in the Grand and Nida Rivers

Distribution of fishes in the Grand River was determined from my own collections and from Ontario Ministry of Natural Resources stream surveys conducted by collectors whose techniques were appropriate (Mahon et al. 1979; Mahon 1981).

For the Nida River drainages, fish distribution was obtained

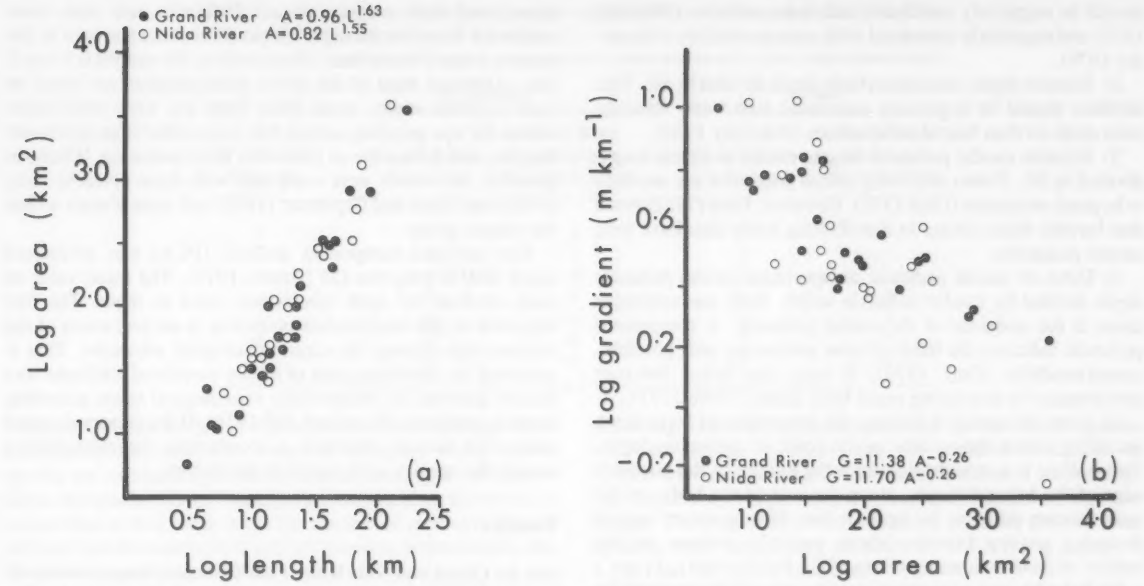


FIG. 3. There are no significant differences in the relationships between (a) drainage area versus main channel length and (b) gradient versus drainage area for streams of the Grand and Nida rivers (Nida River data from Penczak 1971).

primarily from Penczak (1971) supplemented by my collections (Mahon 1981). Penczak (1971) showed the longitudinal distribution of fishes in the eight largest drainages in the Nida River system with the sample localities indicated on the length scale. From these I obtained lists of species collected at 48 localities and the distance of each locality from the source of the river sampled. In both systems, non-native fishes and lampreys were excluded.

Life History Parameters

The species commonly occurring in the two river systems at about 90 km or less from the source are compared on the basis of six parameters, estimates for which were compiled from the literature. The data are mainly for populations geographically close to the study areas. For the species from Poland, most of the data are derived from studies in streams and reservoirs of Poland and Czechoslovakia. For the Ontario species it was frequently necessary to consult studies from Michigan, northern New York, and northern Pennsylvania. However, most of the data were available from studies in the Grand River drainage. The values used are from fish populations in streams, reservoirs, or lakes and are species oriented rather than habitat oriented. Populations from brackish waters, or sea-run fish, were not considered. Further details of the compilation of these data and extensive references are given by Mahon (1981). Following are the six parameters considered.

1) Maximum age (MA): There were sufficient data for most species that the values could be confirmed by more than one study. Only in the case of *Umbra limi* was there any substantial discrepancy among studies. The maximum number of full years of life (annuli recorded) was used.

2) Maximum length (MSL): This indicates the size of individuals in a species. Standard lengths (SL) were used. When only total or fork lengths were available they were considered to be 120 and 110%, respectively, of SL.

3) Age of maturity (AM): The youngest age at which 50% of both males and females of a population were observed to be mature.

4) Reproductive span: Maximum age minus age-of-maturity was used to indicate the length of reproductive life.

5) Fecundity (F): The average number of eggs produced by an individual of the median age in the reproductive span was used wherever possible. In some cases, only an average fecundity for the species was available.

6) Egg diameters (ED): Only values for extruded and hardened eggs were used. Egg diameters were used in the full realization that energy content of egg material varies considerable (Balon 1977; Wooton 1979).

Although mortality is critical in determining life histories, estimates are rarely available for fishes. Pauly (1980) showed that for 175 stocks of fishes, mortality was inversely related to the asymptotic length, estimated from the Von Bertalanffy growth equation. I did not attempt to estimate mortality but assumed an inverse relationship between maximum size and mortality (see also Blueweiss et al. 1978).

Ecomorphology

Of the fish species commonly inhabiting the Grand and Nida river systems at about 90 km or less from the source, 29 and 19, respectively, were selected for ecomorphological analysis. Selection of these species, which were most characteristic of rivers in the above size range, was determined in part by the availability of sufficient specimens. Specimens for 42 species were collected by electrofishing in the Grand and Nida river drainage basins; those of the remaining 6 were obtained from Charles University, Prague. For each species, 12 morphological attributes were determined from 10 specimens, wherever possible, which had been preserved in 4% formaldehyde.

1) Index of compression: maximum body depth divided by maximum body width. This index (called flatness by Gatz)

should be negatively correlated with water velocity (Nikolsky 1933) and negatively correlated with maneuverability (Alexander 1974).

2) Relative depth: maximum body depth divided by SL. This attribute should be negatively associated with water velocity, even more so than lateral compression (Nikolsky 1933).

3) Relative caudal peduncle length: caudal peduncle length divided by SL. Fishes with long caudal peduncles are assumed to be good swimmers (Gatz 1979). However, Hora (1922) noted that benthic fishes living in fast-flowing water also have long caudal peduncles.

4) Index of caudal peduncle compression: caudal peduncle depth divided by caudal peduncle width. Both measurements taken at the midpoint of the caudal peduncle. A compressed peduncle indicates the habit of slow swimming and, possibly, maneuverability (Gatz 1979). It may also affect fast-start performance by increasing mean body depth (Webb 1977).

5) Index of ventral flattening: the proportion of body depth occurring below the midline at the point of maximum depth. The midline is a straight line from the middle of the posterior edge of the hypural bones, along the side of the body, to the most anterior point on the head. In fast-flowing water, ventral flattening enables benthic fish to maintain position on the bottom without swimming (Hora 1930; Hubbs 1941).

6) Relative area of pectoral fin: the area of the pectoral fin divided by body area (estimated by SL times maximum depth). Pectoral fin areas are high among slow swimmers, which use them for maneuvering and braking (Alexander 1974), and among fishes that inhabit fast water and use them to deflect water upwards, thereby maintaining close contact with the substrate (Keenleyside 1962; Jones 1975).

7) Shape of pectoral fin: maximum length of fin divided by maximum width. A long, narrow pectoral fin is expected among fishes that swim a great deal (Keast and Webb 1966; Lindsey 1978).

8) Relative area of caudal fin: as for pectoral fin area (6). Although Lindsey (1978) reported that no observable trend in caudal fin area has been noted, Magnuson (1978) found that among scombroid fishes, species with greater relative caudal area swam farther per tail beat. He concluded that area and thrust were related. Webb (1977) also concluded that large caudal fins were important for fast-start performance, the typical swimming mode of most benthic fishes.

9) Aspect ratio of caudal fin: the square of the maximum vertical distance (span) divided by the area of the caudal fin. Fishes with high caudal fin aspect ratios swim more actively and more continuously than those with low aspect ratios (Keast and Webb 1966; Gatz 1979).

10) Position of the eye: the proportion of head depth that occurs below the middle of the eye. Benthic fishes have dorsal eyes, whereas eyes of nektonic fishes tend to be more lateral (Hora 1922; Aleyev 1969; Gatz 1979).

11) Mouth orientation: coded according to the inclination of a plane that is tangential to the lips when the mouth is open (Gatz 1979). Code 1, dorsal, if the plane faced above the vertical. Code 2, terminal, if the plane was vertical. Code 3, oblique, if the plane faced obliquely downward. Code 4, ventral, if the plane was horizontal. The position of the mouth indicates where the fish is feeding in the water column (Gatz 1979).

12) Size: MSL for the species as estimated in the previous section. Size is related to absolute swimming speed and to stream size (Larimore and Smith 1963; Hynes 1970).

Fins were removed from the fish, placed fully extended on paper, and their outlines traced. Distances and areas were measured from the tracings. Linear measurements were to the nearest 1 mm if more than 100 mm and to the nearest 0.1 mm if less. Although most of the above measurements are based on Gatz's (1979) study, some differ from his. Gatz used coded values for eye position, actual fish sizes rather than maximum lengths, and did not use an index of ventral flattening. Wherever possible, the values were compared with those given by Berg (1965) and Scott and Crossman (1973) and were always within the ranges given.

The principal component analysis (PCA) was performed using BMPD program 4M (Brown 1977). The mean value of each attribute for each species was used as input. The first objective of this multivariate procedure is an evaluation of the relationships among the ecomorphological attributes. This is achieved by combining sets of highly correlated attributes into factors that may be interpretable in ecological terms according to these attributes (Frane and Hill 1976). If the factors do make sense, the second objective is to examine the relationships among the species with regard to the factors.

Results

Are the Grand and Nida River Fish Taxocenes Representative?

Comparison of the species richness and composition of the Grand and Nida rivers with others of their respective regions shows that they are representative. The number of fish species in drainage basins increases with size (Welcomme 1979), which may be measured in several ways (Sepkoski and Rex 1974). Therefore, species richness of drainage basins can only be compared with regard to their relative sizes (Fig. 4). There was sufficient data for rivers of a wide enough range of sizes in

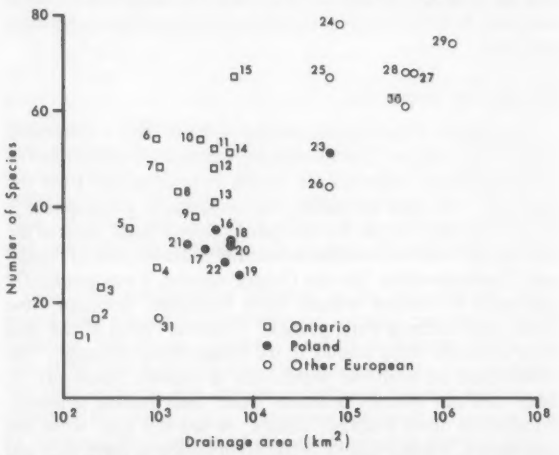


FIG. 4. Relationship between number of species and drainage area for rivers of southern Ontario, Poland, and elsewhere in eastern Europe. Ontario: 1, McIntyre; 2, Neebring; 3, Ganaraska; 4, Sauble; 5, Raisin; 6, Humber; 7, Credit; 8, Au Sable; 9, Maitland; 10, Sydenham; 11, Saugeen; 12, S. Nation; 13, Grand (above Nith); 14, Thames; 15, Grand (all). Poland: 16, Nida (Penczak 1971); 17, Pilica (Penczak 1968b); 18, Warta (Penczak 1969); 19, Lyna (Szczerbowski 1972); 20, Bzura (Penczak 1968a); 21, Raba (Kolder et al. 1975); 22, Drewca (Backiel 1964); 23, Vistula. Other (eastern Europe): 24, Danube; 25, Dniester; 26, Dvina; 27, Dnieper; 28, Don; 29, Volga; 30, Ural; 31, Kysuce (Misik 1959). Data for 1–15 from respective Conservation Authorities and 23–30 from R. L. Welcomme (in. lit.).

TABLE 1. Similarity in faunal composition within similar-sized rivers in Poland (16–22 in Fig. 4) and southern Ontario (8–14 in Fig. 4).

	Ontario		Poland	
No. of rivers compared	No. of species occurring	No. of these occurring in the Grand River	No. of species occurring	No. of these occurring in the Nida River
1	22	1	2	0
2	13	1	3	1
3	8	0	2	1
4	8	5	3	2
5	14	11	5	5
6	10	10	7	7
7	13	13	15	15

southern Ontario to define the species versus drainage area relationship, but most of the rivers in Poland for which lists of species are available are similar in size, making it difficult to define the species versus drainage area relationship. However, it is clear that among these rivers the number of species is similar and less than the numbers of species found in rivers of about the same size in southern Ontario.

To demonstrate that there is a broad relationship between number of species and drainage area in European rivers, I have included six major European rivers and a north Czechoslovakian stream (Fig. 4).

The similarity in fish taxocene composition among similarly sized rivers in each region is shown in Table 1, from which it is clear that the Grand and Nida rivers contain most of the species that are common in their regions. In both regions there are only two species that occur in fewer than four of the seven rivers being compared.

Faunal Composition

The Nida River species (Table 2) comprise about 59% of the 51 species of freshwater fishes found in the Vistula drainage (Rembiszewski and Rolik 1975) and 55% of the 55 species that occur in the Baltic Province (Berg 1965). In contrast, the 36 species from the Grand River (Table 2) comprise only 40% of the 90 species listed for Ontario drainages of Lake Erie (Scott and Crossman 1973) and 27% of the 132 species (excluding introduced species) listed for the Great Lakes (Bailey and Smith 1981).

Cyprinids dominate in both drainages, with 18 (60%) and 15 (42%) species in the Nida and Grand rivers, respectively (Table 2). In the Grand River, the percids, including six species of darters (tribe Etheostomatini), are second in importance (19%) and the centrarchids third (11%). In the Nida River, the noncyprinid species are evenly distributed among the remaining families. In the Grand River, two families endemic to North America, the centrarchids and the ictalurids, and a third, the catostomids, which does not occur in Europe, contribute nine species. Together with the darters, also endemic to North America, these species comprise 42% of the species occurring in the Grand River system.

Species Richness in the Grand and Nida River Systems

In comparing the species richness of two fluvial systems the effects of river size on fish diversity must be considered. Therefore, for each river system the localities were sorted according to distance from source, and the number of species collected (sample richness) and the cumulative number of species were plotted (Fig. 5). The sample richness curves (Fig. 5a) were fitted by regressing the number of species on log river length. The intercepts of the regression lines for the two river systems were signifcantly different ($t = 6.113$, $t_{0.5,(2),82} = 1.989$) but the slopes were not.

Sample species richness is clearly higher in the Grand River by a constant factor at all river sizes. The curves of cumulative number of species diverge more rapidly at small river sizes than do the sample richness curves, and then appear to converge after a stream size of about 60 km in length. The difference in rate of divergence indicates that there may be rapid longitudinal turnover of species composition at these stream sizes and/or replacement of ecologically similar species in similar habitats in different tributaries (Horowitz 1978). Both processes would be reflected in the cumulative diversity curves and further indicate a high diversity of fishes capable of living in small streams in southern Ontario.

Beyond 90 km in length, the rate of accumulation of species in both systems has leveled out. Although by this size the Grand River still has more species the curves have converged, indicating a higher rate of accumulation of species at larger river sizes in the Nida River. This overall pattern indicates that Nida River fishes are more restricted to large rivers than are Grand River fishes.

Habitat Use

To explore the relative proportions of species preferring stream conditions and those preferring lentic habitats but using streams, I placed each species in one of four categories on the basis of the literature (see Mahon 1981) and following a similar classification of Danube River fishes (Holcik and Bastl 1976). Category 1: exclusively fluvial; category 2: primarily fluvial, occasionally lacustrine, including species such as *Notropis cornutus* and *Leuciscus cephalus*, which usually require streams for spawning but can spawn on wave-swept gravel shoals in lakes; category 3: equally fluvial and lacustrine; category 4: primarily lacustrine, occasionally fluvial. This approach is not entirely objective, as fluvial and lacustrine habitats cannot always be clearly distinguished. Backwaters and inundated floodplain lagoons are an integral part of many rivers (Welcomme 1979), and fluvial conditions are closely approximated on rocky lakeshores (Kitchell et al. 1977).

In the Nida River many species are equally or more at home in

TABLE 2. Fish faunas of the Grand River and Nida River systems in streams of 90 km or less, with life history parameters for common species. Data in parentheses were estimated (see Methods). Detailed references to the sources of these data are given by Mahon (1981).

Species (abbrev. in parentheses)	MA (yr)	MSL (mm)	AM (yr)	F (No. of eggs)	ED (mm)
Grand River					
Salmonidae					
Salvelinus fontinalis (Sf)	9	350	4	800	3.5
Umbridae					
Umbra limi (Ul)	4	110	1	735	1.6
Esocidae					
Esox lucius (El)	10	1 000	3	25 000	2.7
Cyprinidae					
Notropis cornutus (Nco)	5	169	1	665	1.5
Notropis rubellus (Nr)	3	62	1	1 090	1.5
Notropis heterolepis (Nh)	2	55	1	650	(1.1)
Rhinichthys atratulus (Ra)	3	58	2	265	0.8
Rhinichthys cataractae (Rc)	5	118	2	5 410	1.0
Pimephales notatus (Pn)	3	78	1	695	1.6
Pimephales promelas (Ppr)	4	73	1	755	1.2
Semotilus atromaculatus (Sa)	5	240	2	3 000	2.2
Semotilus magarita (Sm)	4	132	2	980	0.9
Nocomis spp. (Noc)[a]	6	162	2	555	2.0
Hybognathus hankinsoni (Hh)	4	70	1	(375)	(1.4)
Chrosomus eos (Ce)	3	61	1	500	2.0
Notemigonus crysoleucas (Ncr)	7	211	2	6 020	1.3
Notropis atherinoides (Rare)					
Couesius plumbeus (Rare)					
Catostomidae					
Catostomus commersoni (Cco)	15	487	4	20 000	3.0
Hypentelium nigricans (Hn)	11	292	3	6 070	3.0
Moxostoma sp. (Mox)[b]	10	350	3	21 600	3.2
Ictaluridae					
Noturus flavus (Nf)	9	237	2	975	3.7
Ictalurus nebulosus (In)	8	297	3	7 500	3.0
Gasterosteidae					
Culaea inconstans (Ci)	3	87	1	250	1.3
Centrarchidae					
Micropterus dolomieui (Md)	12	423	4	5 445	2.0
Micropterus salmoides (Ms)	15	453	3	32 820	1.6
Lepomis gibbosus (Lg)	9	219	2	2 303	1.0
Ambloplites rupestris (Ar)	10	222	2	5 500	(1.9)
Percidae					
Etheostoma flabellare (Ef)	4	62	1	225	2.3
Etheostoma caeruleum (Ec)	4	65	1	200	1.8
Etheostoma nigrum (En)	4	60	1	175	1.5
Etheostoma microperca (Em)	2	32	1	85	0.9
Etheostoma exile (Ee)	3	58	(1)	1 620	1.1
Percina maculata (Pm)	4	77	(1)	1 760	2.0
Perca flavescens (rare)					
Cottidae					
Cotus bairdi (Cb)	4	82	2	150	2.2
Nida River					
Esocidae					
Esox lucius (El)	10	1 000	4	25 000	2.7
Cyprinidae					
Leuciscus cephalus (Lc)	15	436	4	30 000	1.9
Leuciscus leuciscus (Lle)	12	234	4	8 000	1.3
Leuciscus idus (Li)	10	396	3	68 500	2.2
Barbus barbus (Bba)	16	550	4	25 000	3.0
Barbus meridionalis (Bm)	6	300	(2)	(13 273)	2.0
Gobio gobio (Gg)	6	142	2	2 880	1.4
Phoxinus phoxinus (Pph)	5	96	2	650	1.4
Rutilus rutilus (Rr)	14	295	4	123 000	1.2
Chondrostoma nasus	14	369	5	8 250	1.7

TABLE 2. (*Concluded*)

Species (abbrev. in parentheses)	MA (yr)	MSL (mm)	AM (yr)	F (No. of eggs)	ED (mm)
Rhodeus sericeus (Rs)	5	80	2	140	1.9
Blicca bjoerkna (Bbj)	16	300	3	41 500	1.7
Tinca tinca (Tt)	9	390	3	40 200	1.9
Abramis brama (Abr)	13	385	4	200 000	1.3
Alburnoides bipunctatus (Abi)	9	129	2	6 000	0.9
Alburnus alburnus (Aa)	10	205	3	5 700	1.5
Scardinius erythropthalmus (Se)	11	290	2	67 160	1.4
Carassius carassius (Cca)	8	222	3	34 700	1.6
Leucaspius delineatus (rare)					
Cobitidae					
Nemacheilus barbatulus (Nb)	5	114	2	5 500	0.9
Cobitis taenia (Ct)	4	87	(1)	1 600	1.8
Sabanajewia aurata (rare)					
Misgurnus fossilis (rare)					
Gadidae					
Lota lota (Llo)	12	711	3	812 280	1.2
Gasterosteidae					
Gasterosteus aculeatus (Ga)	3	61	1	100	1.6
Percidae					
Perca fluviatilis (Pf)	13	290	2	75 000	1.9
Gymnocephalus cernua (Gc)	7	158	2	80 000	1.1
Cottidae					
Cottus gobio (Cg)	5	110	2	350	2.2
Anguillidae					
Anguilla anguilla (catadromous)					
Siluridae					
Silurus glanis (rare)					

[a]Two species.
[b]At least three species.

lacustrine conditions, whereas in the Grand River many are stream specialists (Fig. 6). Indeed, of the 25 species from the Nida River, 9 are sufficiently abundant in lakes in Poland to be fished commercially (Zawisza 1965; Dembinski 1971; Bonar 1977).

Life History

Bionomics

With the exception of egg diameter, the life history parameters (Table 2) are highly intercorrelated (Table 3). A partial correlation coefficient of -0.535 ($N = 52$, $P < 0.1$) shows that egg diameter decreases as (log) fecundity increases when (log) maximum length is held constant. The positive relationship of egg diameter with (log) maximum length masks the trade-off between egg size and fecundity in the simple correlations (Table 3).

Owing to the high degree of correlation among the life history parameters, PCA (BMDP Program 4M, Brown 1977) was used to reduce the number of variables and to ordinate the species (Frane and Hill 1976). To include all species in the ordination, seven missing values (Table 2) were estimated by stepwise regression using the cases for which the data were complete (Brown 1977), but these were omitted when calculating the correlation coefficients.

Reduction of the highly correlated parameters into a single composite variable permits comparison of the communities in one dimension, the first principal component (PC 1), which accounts for 72.2% of the variation in the data (Table 4). The second principal component (PC 2), which accounts for a further 16.2% of the variation, reflects the trade-off between egg diameter and fecundity but consists mostly of the variation in egg diameter (Table 4). The ordination of the species on the first PC shows that large, long-lived, fecund, late-maturing fishes with long reproductive spans are at one extreme and fishes with the opposite combination of characteristics are at the other (Fig. 7a). The former combination of characteristics prevails in the Nida River system whereas in the Grand River there is a preponderance of fishes with the latter combination (Fig. 7a). There is no significant difference in egg diameters between the taxocenes (Fig. 8) ($t = 1.098$, $t_{0.5,29} = 2.458$).

The smoothed (three-interval running average) frequency distributions of species that exhibit some form of parental care, either brood hiding or guarding, and those which do not are compared along PC 1 (Fig. 7b). The overall distribution appears to be bimodal, but only further studies of fluvial fish taxocenes will indicate whether this is an artifact of a two-sample approach or if the modes represent stable combinations, such as suggested by Horn (1978). However, it is clear that parental care is most common among small species (Fig. 7b). This pattern is also common among marine invertebrates (Strathman and Strathman 1982) and coral reef fishes (Barlow 1981).

Reproductive behavior

The quantifiable parameters above must be viewed in light of less easily quantified behaviors such as migration, spawning site preparation or nest building, courtship, tending, and guarding. These adaptations represent a part of the energy cost of reproduction, or reproductive effort (Miller 1979a), which in the case of migration can be substantial (Beamish 1979). Estimates of the caloric costs of these adaptations should be

TABLE 3. Correlations among the life history parameters of fishes from the Grand River and Nida River systems (sample size in parentheses). *$P < 0.05$; ** $P < 0.01$.

	Maximum age	Age of maturity	Reproductive span	Log of fecundity	Egg diameter
Log maximum length	0.860** (57)	0.802** (52)	0.821** (53)	0.804** (55)	0.391** (53)
Maximum age	—	0.842** (53)	0.983** (53)	0.769** (55)	0.270* (53)
Age of maturity		—	0.732** (53)	0.651** (52)	0.318* (50)
Reproductive span			—	0.757** (52)	0.245 (50)
Log of fecundity				—	0.026 (52)

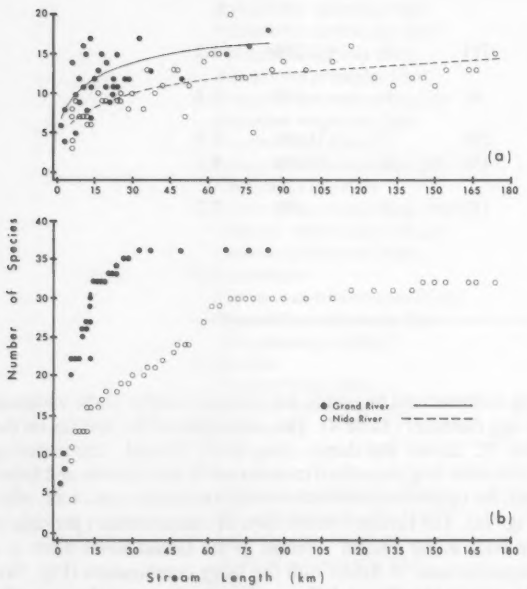


FIG. 5. Comparison of curves of (a) sample species richness and (b) cumulative richness versus river length for the Grand and Nida rivers.

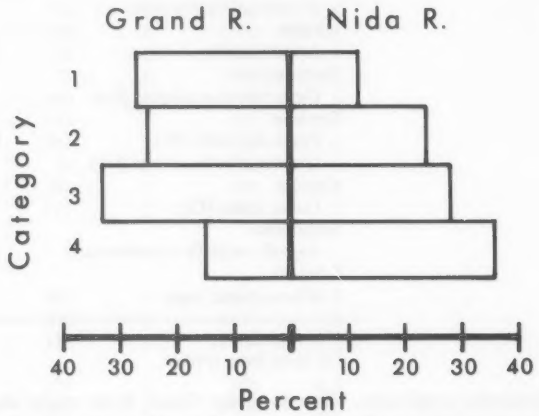


FIG. 6. Percentage occurrence of species in four habitat categories: 1, strictly fluvial; 2, primarily fluvial, occasionally lentic; 3, equally fluvial and lentic; 4, primarily lentic, occasionally fluvial (see text for explanation).

added to the energy content of the gametes, but until they can be quantified, it will be impossible to compare the reproductive effort of species with different reproductive behaviors. However, some progress can be made by grouping the species according to behavior and comparing among groups using the scheme of reproductive guilds of Balon (1975, 1981).

The proportions of species employing each reproductive style differ between the taxocenes (Table 5). In the Grand River, 39.3% of species guard their eggs; only 8% do so in the Nida River drainage. There is a similar protective trend among nonguarders. In the Grand River, about 30% of nonguarders hide their eggs, whereas in the Nida River, only 5% of nonguarders (one species) hide their eggs. There are also differences in the spawning substrate preferences. In the Grand River taxocene, lithophils predominate, and most speleophils nest in cavities under stones, e.g. *Etheostoma flabellare*, *E. nigrum*, *Cottus bairdi*, and *Noturus flavus*. This is consistent with the observed distributions of species in the two communities, as stony substrates are more common in small, fast-flowing streams.

Some of the quantitative differences between the life history parameters of the faunas are associated with the differences in reproductive behavior. Fishes that give parental care are expected to have relatively fewer and larger eggs than those that do not (Williams 1959; Breder and Rosen 1966; Balon 1975), although this has been difficult to demonstrate (Mann and Mills 1979). For these two groups, nonguarding open-substrate spawners and species with parental care (brood hiders and guarders), fecundity is compared after removing the effect of size, as in Fig. 9.

Fishes that give parental care have fewer eggs at a given size than nonguarding open-substrate spawners (Fig. 9). The intercepts of regression lines fitted to these two groups (parental, $F = 0.12MSL^{1.81}$, $N = 21$; nonparental, $F = 0.09MSL^{2.19}$, $N = 34$; both regions combined) differ significantly, but the slopes do not ($P < 0.05$, t-test, Zar 1974). Therefore, the rate of increase in fecundity with size is the same for both groups. However, comparison of the antilogged intercepts (adjusted for lines with a common slope) shows that fishes without parental care have about 5.2 times more eggs at a given size than those with parental care.

A similar result is obtained for the Grand River species only.

TABLE 4. Loadings of the life history parameters on the first two principal components (loadings of less than 0.3 have been replaced by zeros).

	PC 1	PC 2
Maximum age	0.971	0
(Log) maximum length	0.945	0
Reproductive span	0.935	0
Age of maturity	0.882	0
(Log) fecundity	0.837	−0.357
Egg diameter	0.388	0.909
% of total variance (cumulative in parentheses)	72.2 (72.2)	16.2 (88.4)

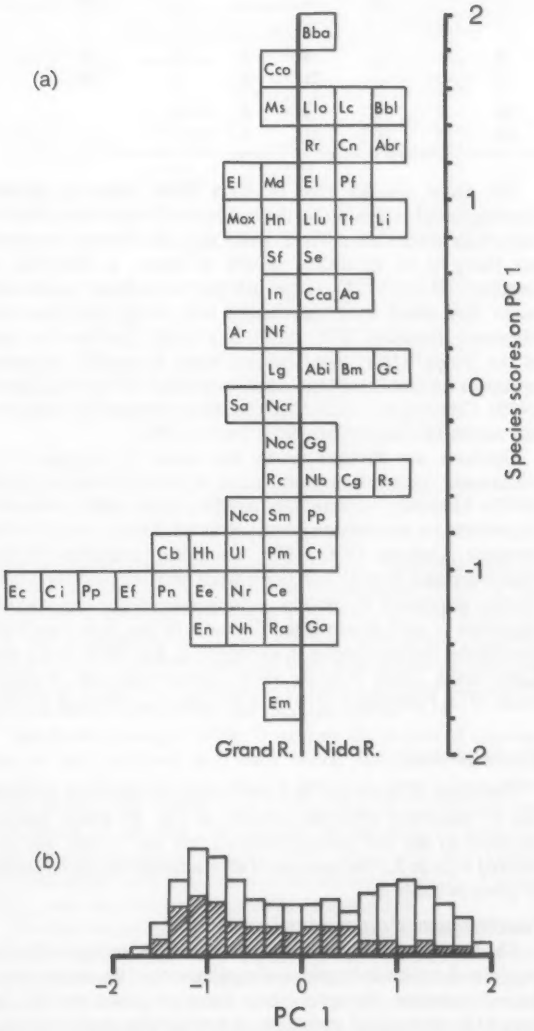


FIG. 7. (a) Ordination of the species (see Table 2 for abbreviations) along the first life history principal component (see Table 3); (b) smoothed frequency distributions along PC 1 of all species (open bars) and of species with parental care (hatched bars).

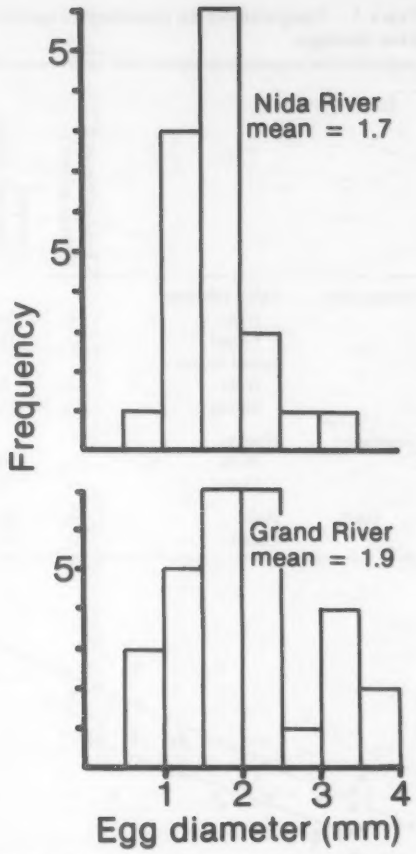


FIG. 8. Frequency distribution of egg diameters for fishes of the two taxocenes.

The intercepts of the regressions are significantly different, but the slopes are not (parental, $F = 0.27MSL^{1.66}$, $N = 12$; nonparental, $F = 0.83MSL^{1.60}$, $N = 14$; $P < 0.05$). Here, the difference in relative fecundity is only 2.3:1.

A comparison between species without parental care in the two communities again reveals significantly different intercepts but not slopes (Nida nonparental, $F = 0.55MSL^{1.92}$, $N = 20$; $P < 0.05$), with the conclusion that in the Nida River, species without parental care have about 3.6 times as many eggs at a given size as those in the Grand River.

The above comparisons demonstrate that fishes that give some care to their eggs are relatively less fecund than those that do not. since this holds true within the Grand River taxocene alone, it is not likely due to some difference between the communities. Given the trade-off between fecundity and egg size, guarders would also have larger eggs than open-substrate spawners, as expected by Williams (1959). Much of the difference in fecundity between the fishes of the two taxocenes is therefore due to differences in size and reproductive behavior. However, since fecundity of nonparental species is lower in the Grand River than in the Nida River (after adjusting for size), other factors should be considered.

Migration

The literature suggests that extensive ontogenetic longitudinal migration or aggregation for spawning prevails among the

TABLE 5. Comparison of the percentage of species employing various reproductive styles in the Nida River and Grand River drainages.

		Litho-pelagophil (larvae pelagic)	Lithophil (stone and gravel)	Phyto-lithophil (intermediate)	Phytophil (vegetation and debris)	Psammophil (sand)	Ostracophil (in molluscs)	Speleophil (in cavities)	Ariadnophil (specialized nest)	Polyphil (indifferent)	Total
Nonguarders	Open substrate										
	Nida	4	24	28	24	8	—	—	—	—	88
	Grand	0	21	6	15	3	—	—	—	—	45
	Brood hiders										
	Nida	—	0	—	—	—	4	—	—	—	4
	Grand	—	15	—	—	—	0	—	—	—	15
Guarders	Nesters										
	Nida	—	0	—	0	—	—	4	4	0	8
	Grand	—	9	—	3	—	—	21	3	3	39
Total	Nida	4	24	28	24	8	4	4	4	0	
	Grand	0	45	6	18	3	0	21	3	3	

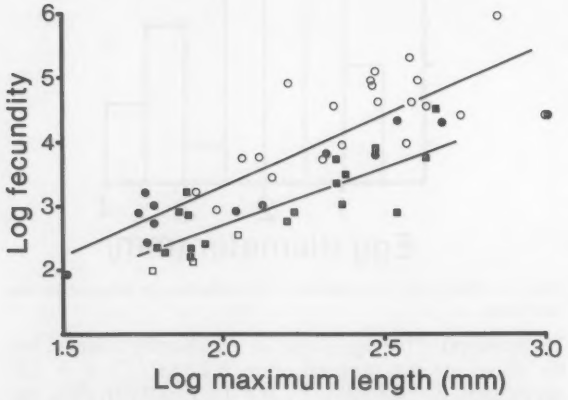


FIG. 9. Relationship between fecundity and length for species from the Grand River and Nida River fish taxocenes. The upper line is for open-substrate spawners (○) and the lower line is for species with parental care (□, Nida River; ■, Grand River).

fishes from Poland whereas small-scale seasonal or irregular migration prevails among those of southern Ontario. Unfortunately, there is insufficient information, particularly in North America, for quantitative evaluation of this impression, and the fact that the degree of migration may vary considerably among populations of the same species (e.g. Holcik and Skorepa 1971; Robbins and MacCrimmon 1977) and among individuals of the same population (e.g. Stott 1961; Funk 1955) further contributes to the problem.

Cyprinids, which are common in European freshwaters, generally aggregate and/or migrate more frequently for spawning than percoid fishes, which are common in North American freshwaters (Breder and Rosen 1966). The latter are more likely to nest and guard (Balon et al. 1977) and consequently to be sedentary and territorial (Perrone and Zaret 1979). However, even within the cyprinids there is a higher incidence of some form of parental care in the Grand River (12% hiders, 19% guarders) than in the Nida River (one hider, no guarders).

The large average size of Nida River fishes is further circumstantial evidence that the incidence of migration is higher there than in the Grand River. Body size and distance migrated are likely to be positively related in fishes, as they are in lampreys (Baker 1978). Large fish can swim faster in absolute terms than small ones and expend less energy per gram per kilometre (Beamish 1978, 1980). In a North Carolina river and in the Volga River, large species more frequently migrated upstream for spawning than small ones (Hall 1972; Poddubnyi 1979). Conversely, small fishes are more frequently sedentary and territorial (Rosenblatt 1963; Barlow 1981).

Opinions are divided as to the extent of migration in warmwater stream fish populations in North America (Hall 1972). However, community studies show that extensive migrations are uncommon among stream fishes in central North America (Gerking 1950, 1953; Thompson and Hunt 1930). Thompson and Hunt (1930) considered only the catostomids to be truly migratory. In contrast, aggregation and/or longitudinal migration is well documented for most of the large cyprinids that inhabit fluvial systems in Europe (e.g. Kaj 1958; Lelek and Libosvarsky 1960; Wheeler 1969; Libosvarsky and Wohlgemuth 1973; Poddubnyi 1979) and for *Lota lota* (Sorokin 1971).

Ecomorphology

The range of body and fin form within the two river systems can be discerned from the outlines in Fig. 10 where species included in the life history analysis but not in this one are marked with an X. The average of each attribute for each species is given in Table 6.

Interpretation of the principal axes

The first two principal components could be interpreted with regard to the assumed ecological significance of the ecomorphological variables. However, these factors together account for only 61% of the total variation. A preliminary analysis found neither mouth position nor caudal fin area to be strongly associated with other variables, and each tended to dominate a principal axis of its own. There was no significant difference between the taxocenes in the proportions of species with each of

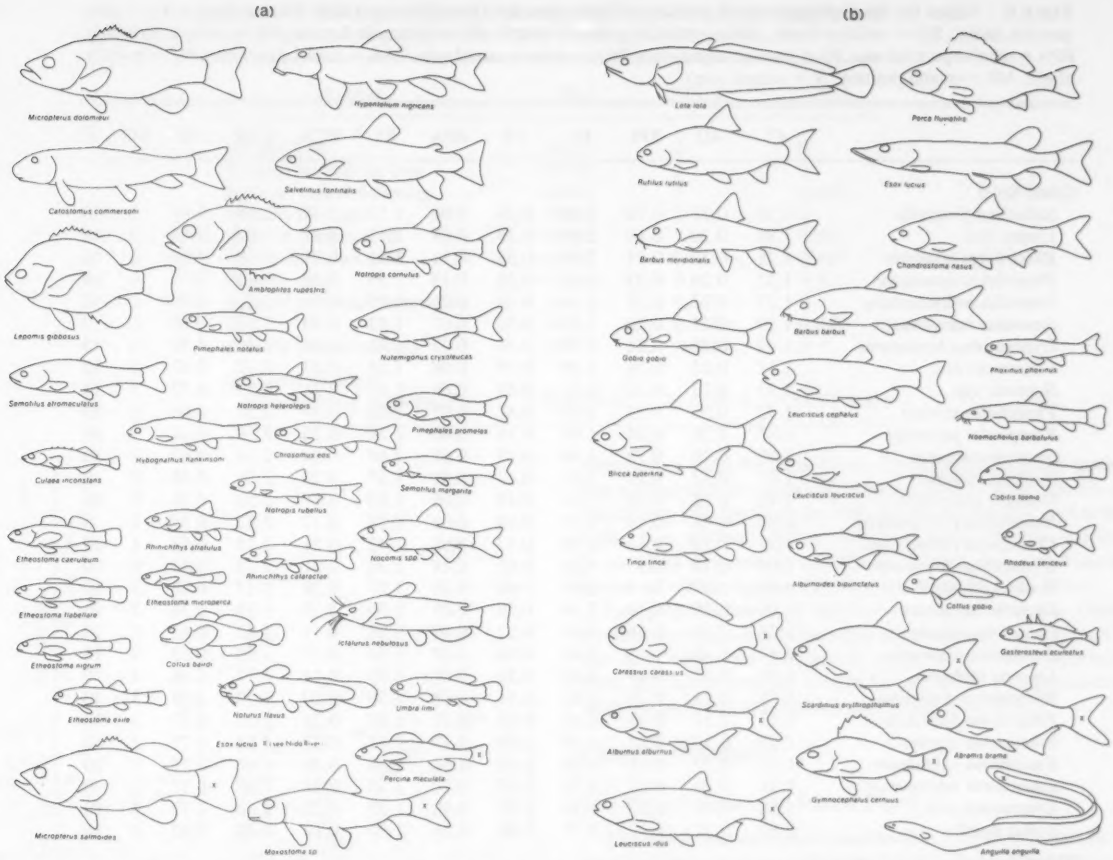


FIG. 10. Diversity of form among species inhabiting drainage basins of about 300 km^2 or less in the Grand River and Nida River systems (species marked with X were not included in the analysis). (a) Grand River system; (b) Nida River system.

the four mouth positions (chi-square = 5.17, tabulated value = 7.82). Relative caudal fin area was significantly larger in the Grand River taxocene ($t = 3.26$, $t_{0.05,(2),19} = 2.09$); however, the lack of association of this attribute with others supports Lindsey's (1978) conclusion that there are no notable trends in caudal fin area (see Methods). Both mouth position and caudal fin area were omitted from the final run (Table 7).

The factor loadings (Table 7) indicate the degree of association of each attribute with each factor. Attributes with high loadings on the same factor usually have high simple correlation coefficients. Only factors with eigenvalues of 1 or greater are considered to account for enough of the total variation to warrant interpretation (Daultry 1973; Frane and Hill 1976). Consequently, only three factors are shown (Table 7). Among these, only the first two are readily interpretable.

The first factor can be interpreted as distinguishing between nektonic fishes of slow-moving waters and benthic fishes from flowing waters. At one extreme would be shallow-bodied, slightly depressed, ventrally flattened fishes with large, pectoral fins, truncate caudal fins, and dorsal eyes. At the other would be deep-bodied, compressed fishes with small, elongate pectoral fins, forked caudal fins, and lateral eyes In the middle would be active, fusiform, nektonic fishes.

The second factor can be interpreted as distinguishing among large, less active swimmers and small active swimmers. It separates large fishes with short compressed caudal peduncles from small fishes with long peduncles, which are circular in cross-section.

The morphological gradient described by the first factor appears to correspond roughly to a gradient in current velocity (Nikolsky 1933; Hora 1930; Hubbs 1941). Similarly, the second factor, in particular the size aspect, would correspond to the gradient of increasing depth, which would be expected in a downstream direction (Larimore and Smith 1963; Hynes 1970). However, as previously mentioned, long, slender caudal peduncles indicate an actively swimming mode of life for nektonic fishes (Lindsey 1978) and habitation of swiftly flowing water for benthic fishes (Hora 1922). Therefore, the second factor also corresponds roughly to a longitudinal gradient in habitat use by the fishes.

Ordination of the fishes

The relative positions of the fishes in the ecomorphological space defined by the first two principal components (Fig. 11) are consistent with the interpretation of the factors. To the upper left of Fig. 11 are species that are typical of slow river reaches and deep pools, whereas to the lower right are species typical of small fast-flowing streams. *Lota lota* is an extreme outlier on the

TABLE 6. Values for the ecomorphological attributes of fishes from the Grand River and Nida River drainages (CI = compression index, RD = relative depth, RPL = relative peduncle length, PC = peduncle flatness, VF = ventral flattening, RPA = relative pectoral area, PS = pectoral aspect ratio, RCA = relative caudal area, CAR = caudal aspect ratio, EP = position of eye, MP = mouth position, *N* = sample size).

	CI	RD	RPL	PC	VF	RPA	PS	RCA	CAR	EP	MP	*N*
Grand River												
Salvelinus fontinalis	1.56	0.22	0.16	1.90	0.49	0.06	1.52	0.18	2.35	0.67	2	10
Umbra limi	1.38	0.20	0.19	2.65	0.59	0.08	1.13	0.22	1.07	0.66	2	10
Rhinichthys atratulus	1.28	0.20	0.24	1.60	0.58	0.11	1.31	0.21	2.30	0.68	3	10
Rhinichthys cataractae	1.22	0.20	0.23	1.41	0.58	0.10	1.39	0.20	2.10	0.72	4	10
Semotilus atromaculatus	1.27	0.22	0.21	1.36	0.49	0.06	1.55	0.19	2.24	0.66	2	10
Semotilus margarita	1.29	0.21	0.22	1.85	0.50	0.07	1.83	0.20	2.11	0.58	2	9
Hybognathus hankinsoni	1.49	0.23	0.21	1.79	0.46	0.06	1.71	0.21	2.10	0.59	3	10
Chrosomus eos	1.51	0.23	0.24	1.89	0.49	0.08	1.54	0.23	2.17	0.57	2	10
Nocomis spp.	1.33	0.23	0.21	1.64	0.48	0.08	1.47	0.21	2.55	0.77	3	10
Pimephales notatus	1.32	0.20	0.23	1.46	0.48	0.07	1.62	0.20	2.57	0.64	3	10
Pimephales promelas	1.47	0.26	0.24	1.88	0.49	0.06	1.76	0.20	2.28	0.64	3	10
Notropis cornutus	1.69	0.20	0.22	1.68	0.47	0.08	1.69	0.24	2.39	0.63	2	10
Notropis rubellus	1.41	0.17	0.21	1.53	0.41	0.09	1.57	0.20	2.50	0.58	2	9
Notropis heterolepis	1.42	0.22	0.26	1.57	0.49	0.06	1.90	0.17	2.50	0.58	3	10
Notemigonus crysoleucas	2.00	0.24	0.18	2.15	0.44	0.05	2.03	0.17	3.42	0.55	1	6
Catostomus commersoni	1.26	0.20	0.14	1.46	0.53	0.08	1.42	0.21	2.13	0.73	4	10
Hypentelium nigricans	1.00	0.19	0.16	1.26	0.61	0.14	1.36	0.21	2.29	0.83	4	10
Noturus flavus	0.91	0.17	0.16	2.89	0.60	0.10	1.07	0.28	1.17	0.86	3	10
Ictalurus nebulosus	1.03	0.26	0.16	2.29	0.59	0.07	1.36	0.20	1.51	0.76	2	10
Culaea inconstans	1.73	0.26	0.18	1.05	0.57	0.07	0.98	0.11	1.62	0.62	2	10
Ambloplites rupestris	2.14	0.40	0.15	2.42	0.50	0.07	1.54	0.17	1.63	0.63	2	10
Lepomis gibbosus	2.36	0.43	0.19	2.08	0.51	0.07	2.08	0.14	1.77	0.66	2	10
Micropterus dolomieui	1.75	0.26	0.20	1.82	0.51	0.08	1.39	0.20	1.79	0.69	2	10
Etheostoma flabellare	1.25	0.17	0.16	2.42	0.53	0.17	1.29	0.24	1.27	0.77	2	10
Etheostoma nigrum	1.25	0.19	0.23	1.40	0.55	0.17	1.67	0.22	1.54	0.77	3	10
Etheostoma caeruleum	1.34	0.20	0.18	1.92	0.56	0.21	1.46	0.20	1.66	0.76	2	10
Etheostoma microperca	1.51	0.20	0.27	1.72	0.57	0.17	1.72	0.24	1.02	0.72	2	10
Etheostoma exile	1.38	0.18	0.25	1.39	0.55	0.18	1.37	0.22	1.42	0.73	3	10
Cottus bairdi	0.68	0.22	0.07	1.97	0.56	0.26	1.36	0.19	1.25	0.92	2	10
Nida River												
Esox lucius	1.35	0.17	0.13	1.64	0.53	0.06	1.45	0.14	1.95	0.79	2	10
Noemacheilus barbatulus	1.11	0.18	0.16	1.88	0.60	0.10	1.23	0.19	1.49	0.83	4	10
Cobitis taenia	1.68	0.14	0.14	2.79	0.50	0.06	1.82	0.20	1.57	0.82	4	4
Leuciscus cephalus	1.55	0.25	0.20	1.90	0.45	0.06	1.71	0.18	2.41	0.59	2	2
Leuciscus leuciscus	1.72	0.23	0.20	1.70	0.47	0.06	1.62	0.19	1.82	0.60	2	10
Rutilus rutilus	2.03	0.31	0.17	1.40	0.50	0.05	1.89	0.17	2.28	0.60	2	10
Phoxinus phoxinus	1.34	0.21	0.24	1.44	0.51	0.09	1.49	0.22	2.34	0.67	2	10
Gobio gobio	1.37	0.22	0.19	1.47	0.50	0.09	1.44	0.19	2.03	0.79	4	10
Chondrostoma nasus	2.21	0.26	0.17	2.25	0.53	0.04	1.78	0.14	2.59	0.53	3	6
Alburnoides bipunctatus	1.88	0.27	0.16	1.66	0.47	0.06	1.58	0.18	3.02	0.57	2	3
Rhodeus sericeus	2.80	0.36	0.22	1.70	0.51	0.03	1.88	0.15	2.35	0.54	3	10
Blicca bjoerkna	2.87	0.37	0.10	3.33	0.50	0.03	2.57	0.29	3.07	0.50	3	10
Barbus meridionalis	1.21	0.22	0.16	1.67	0.49	0.08	1.50	0.18	2.71	0.60	4	4
Barbus barbus	1.46	0.22	0.17	1.69	0.57	0.09	1.47	0.20	2.41	0.74	4	6
Tinca tinca	1.63	0.27	0.14	2.61	0.51	0.05	1.74	0.20	1.41	0.63	2	10
Lota lota	1.04	0.19	0.00	3.02	0.51	0.07	1.35	0.09	0.89	0.82	2	7
Gasterosteus aculeatus	1.84	0.23	0.18	1.00	0.52	0.09	0.92	0.11	1.81	0.60	1	10
Perca fluviatilis	1.73	0.24	0.18	1.46	0.50	0.06	1.45	0.16	1.90	0.72	2	7
Cottus gobio	0.68	0.19	0.10	1.54	0.52	0.25	1.61	0.21	1.52	0.87	2	10

second factor because its peduncle length is zero. Reanalysis without this species made no discernible differences in the factor structure in Table 7 or in the pattern of Fig. 11.

If the Grand River and Nida River taxocenes were ecomorphologically equivalent, species from both rivers should be evenly mixed in the space depicted in Fig. 11. This is not the case; there appear to be more Nida River species to the upper left of the space and more Grand River species to the lower right (Fig. 11). A line of slope 1 through the origin divides the array in two, with 12 Nida River and 8 Grand River species to the upper right and 5 and 21, respectively, to the lower left. On the basis of a chi-square test for homogeneity of these ratios ($\chi^2 = 7.99$, $\chi_{0.01,1} = 6.63$), I reject the null hypothesis of no difference in favor of the alternate hypothesis that the two taxocenes occupy different positions on an ecomorphological axis that appears to correspond to a longitudinal gradient in fluvial habitat use.

TABLE 7. Loadings of the ecomorphological attributes on the first three principal components (loadings of less than 0.3 have been replaced by zeros).

Attribute	PC 1	PC 2	PC 3
Eye position	0.872	0	0
Relative pectoral fin area	0.763	0	0
Index of ventral flattening	0.689	0	0.414
Pectoral fin shape	0.652	0	0
Index of compression	−0.823	0	0.427
Caudal fin aspect ratio	−0.728	0	−0.414
Relative depth	−0.655	0	0.521
Index of peduncle compression	0	0.767	0
Size	0	0.724	−0.441
Relative peduncle length	0	−0.841	0
% of total variance (cumulative in parentheses)	39.8 (39.8)	21.0 (60.8)	11.0 (71.8)

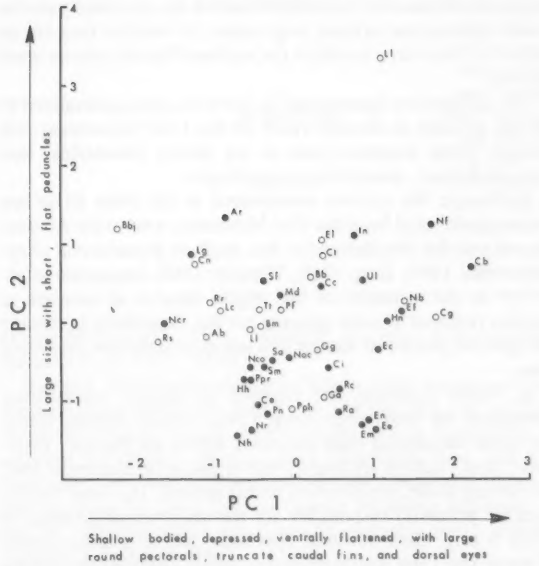

PC 2
Large size with short, flat peduncles
PC 1
Shallow bodied, depressed, ventrally flattened, with large round pectorals, truncate caudal fins, and dorsal eyes

FIG. 11. Relationships among the species of the Grand River (●) and Nida River (○) with regard to the first two principal components (see Table 2 for abbreviations).

Inclusion of the species that were omitted from the analysis would increase the observed difference. Of the seven omitted Nida River species, five are relatively large, deep-bodied, nektonic cyprinids, which typically occur in large rivers (Fig. 10).

Ecological equivalence

Functional ecological equivalence of species is frequently accompanied by morphological similarity (Karr and James 1975) but a direct one-to-one match is seldom to be expected, except in the simplest communities (Orians and Solbrig 1977). Instead, I looked for equivalent groups of species (Diamond 1975), but with little success owing to the absence of distinct clusters of species in Fig. 11. One possible candidate for a cluster appears in the lower centre (between 0 and −1, factor 1) and is composed of small, fusiform, typically small-stream minnows. There are 11 species of which only 1, *Phoxinus phoxinus*, is from the Nida River. To the left, this group grades into a group of eight substrate-oriented, small-stream species of which only two are from the Nida River. Above this, and to the right, is a diverse, diffuse group of eight benthic species, bounded by *Etheostoma caeruleum*, *Umbra limi*, and *Noturus flavus*, of which, again, only two are from the Nida River.

The preponderance of small-stream species in the Grand River is primarily due to the small cyprinids and the darters. On the other hand, the absence of large, deep-bodied cyprinids from the lower reaches of the Grand River is conspicuous, whereas such species predominate in the Nida River.

General Discussion

Life History Patterns in Stream Fishes

This study has revealed considerable overall differences in the life history patterns of stream fishes in Poland and Ontario. The way in which these differences reflect the use of stream habitats by fishes will be discussed first in the context of current views of life history patterns. In both systems, the species with small body size and the associated bionomic traits are primarily those that inhabit small streams. Species with larger body size inhabit large streams primarily but may migrate upstream for short periods to spawn and may remain in small streams as juveniles. The small-sized, small-stream specialists predominate in Ontario, whereas large-sized species with a migratory pattern of habitat use are prevalent in Poland (Fig. 7a).

The positive relationship between stream size and fish size (Thompson and Hunt 1930; Hynes 1970; Patrick 1975) could be caused by size-related mortality or by high total mortality unrelated to size. Size-related mortality could be due to vulnerability to predation by birds (Eipper 1956) and to physical stresses, such as high temperature (Hart 1952) and low oxygen (Lowe et al. 1967), which would occur during periods of low flow. Furthermore, during both flood and drought, small size would facilitate taking refuge under stones or other cover, and in pools. That individuals of many migratory species drop downstream as they increase in size is indicative of a gradient in size-dependent mortality in streams.

The strong correlation between size and longevity suggests that size-independent mortality is also high. Indeed, there is substantial evidence for the view that stream fish taxocenes are in general regulated by unpredictable environmental factors (Moyle and Li 1979; Grossman et al. 1982) and that for fishes the

severity and variability of the physical environment decreases from headwaters downstream (Thompson and Hunt 1930; Hynes 1970; Schlosser 1982). This is so despite the fact that some groundwater-fed, well-forested headwaters, typically inhabited by salmonids, may be more stable than warm downstream reaches. Horwitz (1978) concluded that discharge variability is a primary factor in streams, since discharge not only has direct physical effects but is correlated with temperature, the amounts of dissolved gasses and solids, and pH. He demonstrated an inverse relationship between discharge variability and distance from source, which is consistent with the observation that headwater fishes are more tolerant of abrupt changes in physical conditions, both intra- and inter-specifically, than fishes from downstream habitats (Mathews and Styron 1981). This physical gradient has been interpreted as causing the gradient of species richness in stream fishes (Horwitz 1978), and Tramer (1977) has predicted that life histories of stream fishes should exhibit a gradient of adaptation to increasing density independence and environmental unpredictability upstream.

Life history theory predicts that the combination of small size, early maturity, short life, and short reproductive span should be accompanied by a high allocation of energy to reproduction and by the apportionment of that energy into a large number of minimally provisioned offspring (Stearns 1976; Gould 2977; Horn 1978). However, the life history parameters are assumed to be free to vary together. when one or more of the parameters are constrained in some way, unpredictable combinations may occur (Stearns 1980).

In the stream-dwelling fishes in this study, egg size is probably constrained by extrinsic rather than intrinsic factors. Fish eggs can be considerably smaller (Miller 1979b) than observed in this study, e.g. among pelagic marine fishes (Ware 1975). Large eggs produce large embryos and larvae (Balon 1977; Wooton 1979), which for stream-dwelling fishes may be better able than small larvae to maintain their position in flowing water (Hynes 1970) and to feed on benthic organisms (Kryzhanovsky 1949). Most larval fishes in lotic or pelagic ecosystems eat plankton, but plankton is scarce in flowing water, and benthic organisms of streams are on average larger than most plankton.

Since body size constrains fecundity and there are constraints on minimum egg size, decrease in body size makes each egg a larger investment relative to body size (Miller 1979b) and total egg mass. Parental care by small fishes may then be an appropriate means of further insuring the already high investment in each offspring, particularly if there is a greater tendency to be sedentary and if nesting sites that can be easily defended against egg predators are more available to small fishes.

The two main combinations of life history parameters found in this study appear to be inconsistent with the "accepted scheme," suggesting that fishes will not generally conform to theoretical life history formulations. If small size is caused by high mortality rates (Pauly 1980; Blueweiss et al. 1978) and frequently results in parental care among fishes, then high relative investment per offspring may occur in short-lived, early-maturing fishes as a consequence of small size and habitat constraints and in large, long-lived, late-maturing fishes (e.g. sharks, coelacanth) according to theoretical predictions. Alternatively, large numbers of tiny offspring may be produced by small, short-lived, early-maturing fishes in accord with the "accepted scheme" fishes (see Miller 1979b) and by large species if dispersal is important (Barlow 1981) or if there is access from the adult habitat to one that is unsuitable for adults but appropriate for early life history stages. Examples are upstream versus downstream habitats, estuaries or lagoons versus coastal inshore (Weinstein 1979; Weinstein et al. 1980), and open ocean versus coral reefs (Sale 1978; Johannes 1978). Fishes are particularly suited to this type of ontogenetic shift in habitat use because of their locomotor ability as both adults and young.

How Widely do the Observed Differences Apply to Fluvial Fish Communities in Europe and North America?

The Baltic Sea and Great Lakes fish faunas are subsets drawn from larger faunas in adjacent glacial refugia. Endemism is minimal, restricted largely to lake-dwelling salmoniforms. Consequently, to account for the differences in taxocene structure between the Grand and Nida rivers it is necessary to consider the historical and ecological biogeography of much larger regions. Before proceeding to this broad scale it is important to consider the extent to which the observed patterns can be generalized to these larger areas, or whether they are an artifact of the ways in which the regional faunal subsets were derived.

The differences summarized in Table 8 can be generalized to fluvial systems in Europe (west of the Ural Mountains) and eastern North America (east of the Rocky Mountains) that support diverse, warmwater assemblages.

In Europe the species encountered in the Nida River are widely distributed from the Ural Mountains west to the Atlantic Ocean and the Mediterranean Sea north to Scandinavia (Kryzhanovsky 1949; Berg 1965; Wheeler 1969; Banarescu et al. 1971). In the southeast of this region there is an increase in species richness in some genera, but this is unlikely to change the general picture of stream fish taxocene structure presented here.

In North America, the changes in species composition throughout the Mississippi–Great Lakes–coastal Atlantic region are more substantial than described above for Europe. However, these changes are largely due to species replacement and, on moving south, proliferation within genera. The most prolific taxa are primarily responsible for the observed differences in Table 9 (e.g. darters, small cyprinids, and to a lesser extent *Noturus* spp.) and would more than offset increases in richness of genera such as *Moxostoma* and *Lepomis*, which are typical of the largest streams considered here.

These conclusions are supported by the wide variety of literature on stream fish distribution in both Europe (e.g. Balon 1964, 1968; Holcik et al. 1965; Huet et al. 1969; Daget and Economidis 1975; and previously cited references) and North America (e.g. Trautman 1957; Patrick 1961; Larimore and Smith 1963; Lee et al. 1980; and previously cited references).

Explanations for the Differences in Taxocene Structure

In contrasting the diversity of the European and North American faunas, Gilbert (1976) referred to the "explosive evolution" of the darters and minnows (particularly the genera *Etheostoma* and *Notropis*), which are responsible for most of the diversity in small streams of the Grand River system. Proximate explanations for the extensive speciation of the above-mentioned groups are available. Groups of fishes that are small stream specialists are often highly speciose. Geographic, physical, and biotic factors isolate populations in drainages

TABLE 8. Summary comparison of patterns of diversity, morphology, and life history of Grand River and Nida River fishes.

Characteristic	Grand River	Nida River
Species richness		
Sample richness	Consistently high	Consistently low
Cumulative richness	Consistently high, increases very rapidly in small streams, probably due to lateral or longitudinal species replacement, then levels out	Consistently low with more gradual accumulation, continuing at larger river sizes than in the Grand
Morphology	Small substrate oriented or fusiform nektonic species predominate; typical of small streams	Large, nektonic, deep-bodied species predominate; typical of large rivers
Life history		
Bionomics	Small, short-lived, early-maturing, relatively less fecund species with short reproductive spans predominate	Large, long-lived, late-maturing, relatively fecund species with long reproductive spans predominate
Parental care	Brood hiding, nesting, and guarding are common	Open-substrate spawning with no parental care predominates
Migration	Relatively few species undertake extensive longitudinal migrations or aggregate in large large spawning schools	Many species migrate extensively and form large spawning aggregations

(Lowe-McConnell 1969), resulting in genic differentiation (Echelle et al. 1975, 1976).

The life history adaptations for life in small streams would increase genetic isolation. Small size, territoriality, and reduced dispersal of young would reduce mixing among populations in adjacent tributaries whereas short generation time and the possibility of small minimum population size would increase the potential for rapid genetic change following isolation. A similar situation exists for fishes of isolated, rocky coastal habitats (Rosenblatt 1963).

Although the colonization of small streams by permanent residents may be a proximate reason for high diversity in streams in North America, the ultimate question is why such extensive colonization took place in North America but not in Europe. Small warmwater streams are physically rigorous and variable (Hynes 1970; Horwitz 1978; Schlosser 1982), and I suggest that they would seldom be colonized by species establishing permanent, local populations. Unless some factor prevents it, selection would favor the option of migration. The overall differences between the studied taxocenes and the similar life history patterns among the darters and fluvial cyprinids in the Grand River suggest that such a factor was more influential in eastern North America than in Europe.

Discounting the possibility that the streams of Europe are, on the whole, more navigable by fishes and/or less hospitable than those of eastern North America, there are three types of major factors to be considered: first, the original lineages from which the taxocenes evolved, second, the large-scale interactions of historical climatic changes with topography, and third, biotic effects of historical differences in faunal composition.

Ancestral similarity

The early ancestral cyprinid and percid groups from which the small minnows and darters proliferated were available in both regions. Collette and Banarescu (1977) suggested that the darters invaded the previously unexploited habitats in small streams and became adapted to local conditions there. These habitats were, presumably, also available in European streams but were not similarly exploited. The subfamily Percinae, to which the darters belong, is widespread in Europe, and furthermore, the four species of the tribe Romanichthyini (Percidae, Lucioperinae) show many adaptations to stream life, similar to those of the darters (Collette and Banarescu 1977). Yet, extensive speciation did not occur in Europe.

Hynes (1970) suggested that the loaches (Cobitidae), which are restricted to Eurasia, are ecological analogs to the darters of which about 153 species in 3 genera have been described (Collette and Banarescu 1977). In Europe there are 23 species of cobitids: 12 *Nemacheilus*, 9 *Cobitis*, and 1 each of *Misgurnus*, *Sabanajewia*, and *Turcinemachelus*. The Cobitidae and Etheostomatini are similar in that many species are restricted to small streams and have small geographical ranges; only *Cobitis taenia*, *Sabanajewia aurata*, *Nemacheilus barbatulus*, and *Misgurnus fossilis* are widely distributed in European freshwaters (Banarescu et al. 1971). However, the degree of speciation that this group has undergone does not appear to be comparable with that of the darters.

Similarly, the European cyprinids did not often diversify in the vacant "resident" niches in small streams there. All but a few species of the eastern North American cyprinids that have become so successful in streams are believed to have arisen

from the cyprinid subfamily Leuciscinae. Genera of this subfamily are successful inhabitants of fluvial systems in Europe but are relatively large and tend to migrate up and down stream seasonally.

Topography and climate

Differences in patterns of glaciation and redispersal must be considered as a factor contributing to relatively high diversity in small streams in North America. Although the sequence and timing of glacial advance and retreat during the Pleistocene were similar in Europe and North America (Flint 1971), the Mississippi basin and the Atlantic drainages provided a much larger total refugial area for freshwater fishes than did the Danube and other drainage systems of the Black and Caspian seas. On this basis, and on the basis of absolute overall size, substantial differences in species richness would be expected between Europe and eastern North America. Moyle and Cech (1982) suggested that the partial isolation of the many tributaries in the Mississippi River system may have contributed to this richness. In contrast, the river systems of Europe are even more isolated, frequently separated by salt water. However, the question is not a straightforward difference in species richness; it is the degree of speciation amongst fishes inhabiting small streams. In eastern North America the highest density of stream species is in the center of the Mississippi basin; in Europe it is in streams around the Black and Caspian seas (Kryzhanovsky 1949; Banarescu et al. 1971; Banarescu 1975). However, even in the latter area, stream-dwelling species do not show the degree of miniaturization and development of parental care common among small-stream percids and cyprinids in eastern North America (Kryzhanovsky 1949).

Conceivably, the degree of isolation of European river systems and the east–west barriers to easy movement in and out of glacial refugia could have prevented the accumulation of species. Small-stream specialists would disperse and retreat more slowly than large migratory species. Colonization would be less frequent and extinction more frequent under conditions of extremely restricted movement. However, it is not clear why a greater degree of small-stream specialization did not develop within the main refugial areas of Europe.

Biotic differences

In eastern North America, in addition to the relict lentic specialists, the gars (Lepisosteidae) and bowfin (Amiidae), there are two families of freshwater fishes of which most species inhabit slow rivers and lakes: the Centrarchidae and the Ictaluridae. Members of both are predatory with advanced styles of reproduction: nesting and guarding. Although some ictalurids, primarily in the genus *Noturus*, have successfully invaded small streams, the centrarchids generally have not, except as pool dwellers and occasionally as seasonal migrants. The basic body plan of most centrarchids is unsuited to flowing water, but they dominate in slow-flowing and lentic waters. Collette et al. (1977) suggested that the centrarchids are responsible for the scarcity of large, lacustrine percids in North America.

The presence of lentic specialists such as the centrarchids and perhaps the ictalurids could have been decisive in preventing many species from adopting the preferred migratory pattern of fluvial habitat use by weighting the odds towards the option of specializing for life in small streams exclusively. In Panama, the impact of a newly introduced piscivore was much greater in Gatun Lake than in tributary rivers (Zaret 1979). During the original invasion and radiation of ancestral centrarchids into lakes and lowland rivers, they must have displaced the riverine species upstream, forcing an increasing degree of adaptation to fluvial conditions.

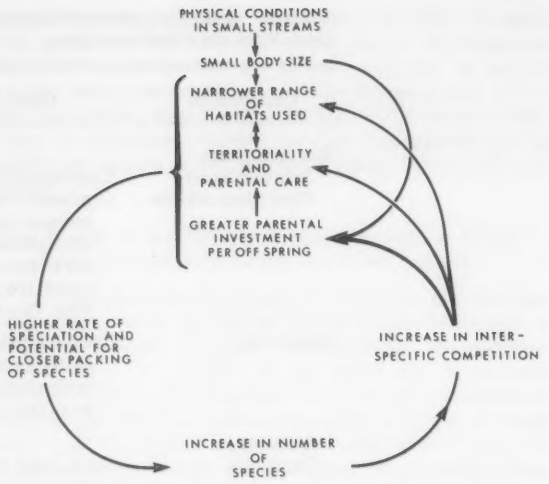

PHYSICAL CONDITIONS IN SMALL STREAMS
SMALL BODY SIZE
NARROWER RANGE OF HABITATS USED
TERRITORIALITY AND PARENTAL CARE
GREATER PARENTAL INVESTMENT PER OFF SPRING
HIGHER RATE OF SPECIATION AND POTENTIAL FOR CLOSER PACKING OF SPECIES
INCREASE IN INTER-SPECIFIC COMPETITION
INCREASE IN NUMBER OF SPECIES

FIG. 12. Feedback loop promoting an increase in diversity in stream fish taxocenes. The adaptations to permanent life in small streams would favor speciation.

Percids did not have a similar effect in European waters primarily because they are secondarily lacustrine and, therefore, not directly analogous to the centrarchids. Kitchell et al. (1977) postulated that percids are most successful in lentic systems where they have access to fluvial spawning grounds, or where fluvial conditions are approximated on turbulent shores and shoals. Consequently, they explained, percids are outcompeted by cyprinids in warm eutrophic waters in Europe and by centrarchids in North America.

Implications for Stream Fish Community Structure

It appears that the differences between the two regions are a consequence of displacement of fishes in eastern North America up into small streams and that adaptation to the conditions there contributed to speciation and promoted diversity. However, the consequences of increased species richness that would be predicted from ecological theory are similar to those that distinguish the two taxocenes. When diversity is low, intraspecific competition promotes the use of a wide range of habitats. Increased species richness could change the balance between intra- and inter-specific competition and decrease the range of habitats used per species (Cody 1974). Thus, a shift from mobile or migratory towards sedentary species would be expected. Consequently, territoriality and parental care should become more common. Considering the relationship between body size and home range for fishes (Sale 1978), small body size could also reduce the range of habitats (resources) used and permit more species to coexist on a given range of resources (Lindsey 1966).

The above mechanisms would provide positive feedback between the adaptations contributing to the development of diversity and the effect of increased diversity on the development of those adaptations (Fig. 12). According to this scheme the development of diversity should be precipitous. However, there are countermechanisms such as the costs of adapting to high density-independent, and probably size-dependent, mor-

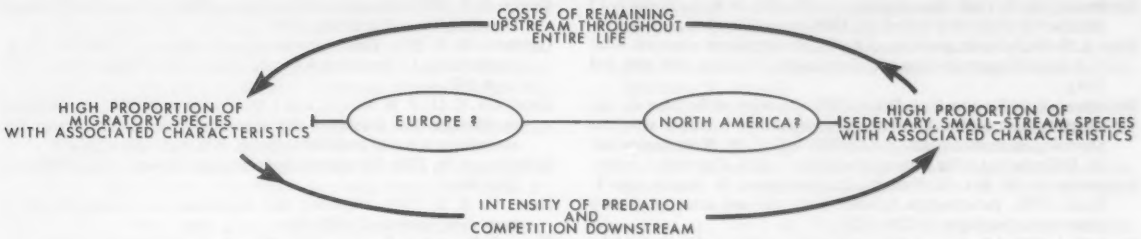

COSTS OF REMAINING UPSTREAM THROUGHOUT ENTIRE LIFE
HIGH PROPORTION OF MIGRATORY SPECIES WITH ASSOCIATED CHARACTERISTICS
EUROPE ?
NORTH AMERICA ?
HIGH PROPORTION OF SEDENTARY, SMALL-STREAM SPECIES WITH ASSOCIATED CHARACTERISTICS
INTENSITY OF PREDATION AND COMPETITION DOWNSTREAM

FIG. 13. Hypothetical equilibrium model of stream fish taxocene diversity and structure.

tality in streams. As populations become smaller in size and total area occupied, the probability of extinction increases. Also, the population efficiency of resource utilization would decrease with the establishment of local populations in habitats with high density-independent mortality. As the population structure shifts towards young ages and small individual size, less total biomass can be maintained on a given energy resource (Banse and Mosher 1980) and the population becomes more susceptible to chance extinction.

Therefore, the proportions of mobile and sedentary species in a stream taxocene will probably be determined by the relative costs of density-independent mortality incurred by remaining upstream all year and the costs of predation, competition, and migration incurred by moving downstream. The hypothesized system of opposing factors is depicted in Fig. 13. These costs will differ with river basin morphology, climate, and faunal composition. This study suggests that the last of these has the potential to produce considerably different taxocene structures in river systems that are similar with regard to the first two factors.

Conclusions

The initial hypothesis that fish taxocenes in physically similar river systems in Poland and Ontario are similar in structure is rejected. This conclusion lacks rigor in a statistical sense, since there are no conclusive tests for "significant" differences between taxocenes. Furthermore, the assumptions necessary for a valid hypothesis of convergence between taxocenes are seldom satisfied (Cody and Mooney 1978). However, the differences between the river systems were sufficiently clear and consistent between the various levels of organization that the question "how different is different" was not an issue.

There were several possible reasons for the differences, ranging from the effects of large scale topography on ease of dispersal and retreat to the influence of lentic specialists in forcing fishes to adapt permanently to small streams rather than migrate seasonally. The findings of this study emphasize the possible roles of climatic, geological, and biotic historical events in producing divergent taxocene structure in similar present-day environments.

Acknowledgments

Above all I thank Eugene Balon for his encouragement and advice throughout. He suggested the comparison of new and old world stream fish taxocenes and introduced me to the rich east-central European literature on stream fishes. The work in Poland was made possible by assistance from Tad Penczak, Maciej Zalewski, Marek Molinski, Ewa Suszycka, and Piotr Frankiewiez. Financial assistance was provided by the University of Lodz and coordinated by Tad Penczak. Karel Pivnicka supplied specimens from Charles University, Prague. In Canada the field work was ably lightened by Cam Portt, Susan Mahon, Sam Nsembukya-Katuramu, and Larry Halyk. Many people contributed to the development of this study at a variety of stages: Bill Beamish, Fred Cichocki, Mike Chadwick, Ed Crossman, Hugh Dale, Larry Halyk, Jan Hines, Cass Lindsey, Mike Paine, and Maciej Zalewski. Reviews of part or all of the manuscript by Susan Mahon, Richard Mann, Bill Matthews, Peter Moyle, Ram Myers, and Andy Rosenberg are much appreciated. Extensive review by and discussion with Wayne Hunte played an important role. The study was supported by a NSERC operating grant to Eugene Balon.

References

ALEXANDER, R. MCN. 1974. Functional design in fishes. Hutchinson and Co., Ltd., London. 160 p.

ALEYEV, YU. G. 1969. Function and gross morphology in fish. Israel Program for Scientific Translations, Jerusalem.

BACKIEL, T. 1964. Fish populations in the Drewca River system. Rocz. Nauk Roln. 84: 193–214. (In Polish with English summary)

BAILEY, R. M., AND G. R. SMITH. 1981. Origin and geography of the fish fauna of the Laurentian Great Lakes basin. Can. J. Fish. Aquat. Sci. 38: 1539–1561.

BAKER, R. R. 1978. The evolutionary ecology of animal migration. Hodder and Stoughton Ltd., Kent, England. 1012 p.

BALON, E. K. 1964. Verzeichnis and ökologische charakteristik der fische der Donau. Hydrobiologia 24: 441–451.

1968. Urgeschichte der Donau-Ichthyofauna (vor dem Einfluss seitens des menschen). Arch. Hydrobiol. Suppl. 34: 204–227.

1975. Reproductive guilds of fishes: a proposal and definition. J. Fish. Res. Board Can. 32: 821–864.

1977. Early ontogeny of *Labeotrophus* Ahl, 1927 (Mbuna, Cichlidae, Lake Malawi), with a discussion on advanced protective styles in fish reproduction and development. Environ. Biol. Fishes 2: 147–176.

1981. Additions and amendments to the classification of reproductive styles in fishes. Environ. Biol. Fishes 6: 377–389.

BALON, E. K., W. T. MOMOT, AND H. A. REGIER. 1977. Reproductive guilds of percids: results of the paleogeographical history and ecological succession. J. Fish. Res. Board Can. 34: 1910–1921.

BANARESCU, P. 1975. Principles and problems of zoogeography. Translated and published for the U.S. Dep. of Commerce and the National Science Foundation by NOLIT Publishing, Belgrade. 225 p.

BANARESCU, P., M. BLANK, J.-L. GAUDET, AND J. C. HUREAU. 1971. European inland water fish. Fishing News (Books) Ltd., London. 24 p.

BANSE, K., AND S. MOSHER. 1980. Adult body mass and annual production/biomass relationships of field populations. Ecol. Monogr. 50: 335–379.

BARLOW, G. W. 1981. Patterns of parental investment, dispersal, and size among coral reef fishes. Environ. Biol. Fishes 6: 65–86.

BEAMISH, F. W. H. 1978. Swimming capacity, p. 101–187. *In* W. S. Hoar and D. J. Randall [ed.] Fish physiology, Vol. VII. Locomotion. Academic Press, New York, NY.

1979. Migration and spawning energetics of the anadromous sea lamphrey, *Petromyzon marinus*. Environ. Biol. Fishes 4: 3–7.

1980. Swimming performance and oxygen consumption of the charrs, p. 739–748. *In* E. K. Balon [ed.] Charrs, salmonid fishes of the genus *Salvelinus*. Dr. W. Junk bv Publishers, The Hague.

BECKINSALE, R. P. 1969. River regimes, p. 176–192. *In* R. J. Chorley [ed.] Introduction to physical hydrology. Methuen and Co., Ltd., London.

BERG, L. S. 1965. Freshwater fishes of the USSR and adjacent countries. Vols. 1–3. Israel Program for Scientific Translations, Jerusalem. 504, 496, and 510 p.

BEVERTON, R. J. H., AND S. J. HOLT. 1959. A review of the lifespans and mortality rates of fish in nature and their relation to growth and other physiological characteristics, p. 142–180. *In* G. E. W. Wolstenholme and M. O'Conner [ed.] The lifespan of animals. J. & A. Churchill, London.

BLUEWEISS, L., H. FOX, V. KUDZMA, D. NAKASHIMA, R. PETERS, AND S. SAMS. 1978. Relationships between body size and some life history parameters. Oecologia 37: 257–272.

BOCK, W. J. 1977. Adaptation and the comparative method, p. 57–82. *In* M. K. Hecht, P. Goody, and B. Hecht [ed.] Major patterns in vertebrate evolution. Plenum Press, New York, NY.

BONAR, A. 1977. Relations between exploitation, yield, and community structure in Polish pike perch (*Stizostedion lucioperca*) lakes. J. Fish. Res. Board Can. 34: 1576–1580.

BREDER, C. M. JR., AND D. E. ROSEN. 1966. Modes of reproduction in fishes. TFH Publications, Jersey City, NJ. 941 p.

BROWN, M. B. [ED.] 1977. BMDP biomedical computer programs, P-series. University of California Press, Los Angeles, CA. 800 p.

BROWZIN, B. S. 1962. On the classification of rivers in the Great Lakes–St. Lawrence basin. Publ. Great Lakes Res. Inst. 9: 86–92.

CODY, M. L. 1974. Competition and the structure of bird communities. Princeton University Press, Princeton, NJ. 318 p.

CODY, M. L., AND H. A. MOONEY. 1978. Convergence versus non-convergence in Mediterranean climate ecosystems. Annu. Rev. Ecol. Syst. 9: 265–321.

COLLETTE, B. B., M. A. ALI, K. E. F. HOKANSON, M. NAGIEC, S. A. SMIRNOV, J. E. THORPE, A. H. WEATHERBY, AND J. WILLEMSEN. 1977. Biology of the percids. J. Fish. Res. Board Can. 34: 1890–1899.

COLLETTE, B. B., AND P. BANARESCU. 1977. Systematics and zoogeography of fishes of the family Percidae. J. Fish. Res. Board Can. 34: 1450–1463.

CONSTANTZ, G. D. 1981. Life history patterns in desert fishes, p. 237–281. *In* R. J. Naiman and D. L. Soltz [ed.] Fishes in North American deserts. John Wiley & Sons, New York, NY.

CUSHING, C. E., C. D. MCINTYRE, J. R. SEDELL, K. W. CUMMINS, G. W. MINSHALL, R. C. PETERSEN, AND R. L. VANNOTE. 1980. Comparative study of physical–chemical variables of streams using multivariate analyses. Arch. Hydrobiol. 89: 343–352.

DAGET, J., AND P. S. ECONOMIDIS. 1975. Richesse spécifique de l'ichtiofaune de Macédione orientale et de Thrace occidentale (Gréce). Bull. Mus. Natl. Hist. Nat. Ecol. Gen. 27: 81–84.

DAULTRY, S. 1973. Principal components analysis. Catmog 8. Geo Abstracts, Norwich. 51 p.

DEMBINSKI, W. 1971. Vertical distributions of vendace *Coregonus albula* L. and other pelagic fish species in some Polish lakes. J. Fish Biol. 3: 341–357.

DIAMOND, J. M. 1975. Assembly of species communities, p. 342–44. *In* M. L. Cody and J. M. Diamond [ed.] Ecology and evolution of communities. The Belknap Press of Harvard University Press, Cambridge, MA.

ECHELLE, A. A., E. F. ECHELLE, M. H. SMITH, AND L. G. HILL. 1975. Analysis of genic continuity in a headwater fish, *Etheostoma radiosum* (Percidae). Copeia 1975: 197–204.

ECHELLE, A. A., E. F. ECHELLE, AND B. A. TABER. 1976. Biochemical evidence for congeneric competition as a factor restricting gene flow between populations of a darter (Percidae: *Etheostoma*). Syst. Zool. 25: 228–235.

EIPPER, A. W. 1956. Differences in vulnerability of the prey of nesting kingfishers. J. Wildl. Manage. 20: 177–183.

FLINT, R. F. 1971. Glacial and quaternary geology. John Wiley & Sons, New York, NY. 892 p.

FRANE, J. W., AND M. HILL. 1976. Factor analysis as a tool for data analysis. Community Stat. Theor. Methods A5: 487–506.

FUNK, J. L. 1955. Movement of stream fishes in Missouri. Trans. Am. Fish. Soc. 85: 39–57.

GATZ, A. J. JR. 1979. Ecological morphology of freshwater stream fishes. Tulane Stud. Zool. Bot. 21: 91–124.

GERKING, S. D. 1950. Stability of a stream fish population. J. Wildl. Manage. 14: 194–202.

1953. Evidence for the concepts of home range and territory in stream fishes. Ecology 34: 347–365.

GILBERT, C. R. 1976. Composition and derivation of the North American fish fauna. Fla. Sci. 39: 104–111.

GORMAN, O. T., AND T. R. KERR. 1978. Habitat structure and stream fish communities. Ecology 59: 507–515.

GOULD, S. J. 1977. Ontogeny and phylogeny. Belknap Press of the Harvard University Press, Cambridge, MA.

GREGORY, K. J. 1976. Drainage networks and climate, p. 289–315. *In* E. Derbyshire [ed.] Geomorphology and climate. John Wiley & Sons, New York, NY.

GROSSMAN, G. O., P. B. MOYLE, AND J. O. WHITAKER JR. 1982. Stochasticity in structural and functional characteristics of an Indiana stream fish assemblage: a test of community theory. Am. Nat. 120: 423–454.

GURNELL, A. M. 1978. The dynamics of a drainage network. Nord. Hydrol. 9: 293–306.

HALL, C. A. S. 1972. Migration and metabolism in a temperate stream ecosystem. Ecology 53: 585–604.

HARE, F. K., AND J. E. HAY. 1974. The climate of Canada and Alaska, p. 49–192. *In* R. A. Bryson and F. K. Hare [ed.] Climates of North America. World survey of climatology. Vol. II. Elsevier Scientific Publishing Co., New York, NY.

HART, J. S. 1952. Geographic variations of some physical and morphological characters in certain freshwater fish. Publ. Ont. Fish. Res. Lab. 72: 79 p.

HESPENHEIDE, H. A. 1973. Ecological inferences from morphological data. Annu. Rev. Ecol. Syst. 4: 213–229.

HOLCIK, J., AND I. BASTL. 1976. Ecological effects of water level fluctuations upon the fish populations in the Danube River floodplain and Czechoslovakia. Acta Sci. Nat. Acad. Sci. Bohemoslov. Brno 10: 1–46.

HOLCIK, J., V. MISIK, I. BASTL, AND A. KIRKA. 1965. Fishes of the Orava Valley reservoir and its tributaries. Acta Rerum Nat. Mus. Natl. Slov. Bratis. 11: 93–139. (In Slovak with English summary)

HOLCIK, J., AND V. SKOREPA. 1971. Revision of the roach *Rutilus rutilus* (Linnaeus, 1758), with regard to subspecies. Annot. Zool. Bot. 64: 1–60.

HORA, S. L. 1922. Structural modifications in the fish of mountain torrents. Rec. Indian Mus. (Calcutta) 24: 31–61.

1930. Ecology, biomonics, and evolution of the torrential fauna, with special reference to the organs of attachment. Philos. Trans. R. Soc. Lond. B Biol. Sci. 218: 171–282.

HORN, H. S. 1978. Optimal tactics of reproduction and life history, p. 411–429. *In* J. R. Krebs and N. B. Davies [ed.] Behavioural ecology, an evolutionary approach. Blackwell Scientific Publications, London.

HORWITZ, R. J. 1978. Temporal variability patterns and the distributional patterns of stream fishes. Ecol. Monogr. 48: 307–321.

HUBBS, C. L. 1941. The relation of hydrological conditions to speciation in fishes, p. 182–195. *In* A symposium on hydrobiology. University of Wisconsin Press, Madison, WI.

HUET, M., A. LELEK, J. LIBOVARSKY, AND M. PENAZ. 1969. Contributions à l'identification des zones piscicoles de quelques cours d'eau de Moravie (Tchecoslovagie). Verh. Int. Ver. Limnol. 17: 1103–1111.

HYNES, H. B. N. 1970. The ecology of running waters. Liverpool University Press, Liverpool. 555 p.

JOHANNES, R. E. 1978. Reproductive strategies of coastal marine fishes in the tropics. Environ. Biol. Fishes 3: 65–84.

JONES, A. N. 1975. A preliminary study of fish segregation in salmon spawning streams. J. Fish Biol. 7: 95–104.

KAJ, J. 1958. Spawning of fish in the lower stretch of the Welna River. Pol. Arch. Hydrobiol. 4: 183–192.

KARR, J. R., AND R. C. JAMES. 1975. Ecomorphological configurations and convergent evolution in species communities, p. 258–291. *In* M. C. Cody and J. M. Diamond [ed.] Ecology and evolution of communities. The Belknap Press of Harvard University Press, Cambridge, MA.

KEAST, A., AND D. WEBB. 1966. Mouth and body form relative to feeding ecology in the fish fauna of a small lake, Lake Opinicon, Ontario. J. Fish. Res. Board Can. 23: 1845–1874.

KEENLEYSIDE, M. H. A. 1962. Skin-diving observations of Atlantic salmon and brook trout in the Miramichi River, New Brunswick. J. Fish. Res. Board Can. 19: 624–634.

KITCHELL, J. F., M. G. JOHNSON, C. J. MINNS, K. H. LOFTUS, L. GREIG, AND C. H. OLVER. 1977. Percid habitat: the river analogy. J. Fish. Res. Board Can. 34: 1936–1940.

KOLDER, W., S. SKORA, AND J. M. WLODEK. 1975. Ichthyofauna of the River Raba and of its tributaries. Acta Hydrobiol. 16: 65–99.

KRYZHANOVSKY, S. G. 1949. Ecomorphological principles of development among carps, loaches, and catfishes. II. Ecological groups of fishes and patterns of their distribution. Tr. Inst. Morfol. Zhivotn. Severtsova L: 237–331. (In Russian, translated from Russian by Fish. Res. Board Can. Transl. Ser. No. 2945, 1974)

LARIMORE, R. W., AND P. W. SMITH. 1963. Fishes of Champaign county, Illinois, as affected by 60 years of stream changes. Ill. Nat. Hist. Surv. Bull. 29: 299–382.

LAW, R. 1979. Ecological determinants in the evolution of life histories, p.

81–103. *In* R. M. Anderson, B. D. Turner, and L. R. Taylor [ed.] Population dynamics. Blackwell Scientific Publications, London.

LEE, D. S., C. R. GILBERT, C. H. HOCUTT, R. E. JENKINS, D. E. MCALLISTER, AND J. R. STAUFFER JR. 1980. et seq. Atlas of North American freshwater fishes. North Carolina State Museum of National History, Raleigh, NC. 854 p.

LELEK, A., AND J. LIBOSVARSKY. 1960. The occurrence of fish in a fish ladder in Dyje River near Breclav. Zool. Listy 9: 293–308.

LIBOSVARSKY, J., AND E. WOHLGEMUTH. 1973. Estimates of abundance of fishes in Olsava Creek, with respect to a long winter. Zool. Listy 33: 73–83.

LINDSEY, C. C. 1966. Body sizes of poikilotherms at different latitudes. Evolution 20: 456–465.

1978. Form, function, and locomotory habits in fish, p. 1–100. *In* W. S. Hoar and D. J. Randall [ed.] Fish physiology. Vol. III. Locomotion. Academic Press, New York, NY.

LOWE, C., D. HINDS, AND E. HALPERN. 1967. Experimental catastrophic selection and tolerances to low oxygen concentration in native Arizona freshwater fishes. Ecology 48: 1013–1017.

LOWE-MCCONNELL, R. H. 1969. Speciation in tropical freshwater fishes. Biol. J. Linn. Soc. 1: 51–775.

MAGNUSON, J. J. 1978. Locomotion by scombrid fishes: hydromechanics, morphology, and behavior, p. 240–315. *In* W. S. Hoar and D. J. Randall [ed.] Fish physiology. Vol. VII. Locomotion. Academic Press, New York, NY.

MAHON, R. 1981. Patterns in the fish taxocenes of small streams in Poland and Ontario. Ph.D. thesis, University of Guelph, Guelph, Ont. 297 p.

MAHON, R., E. K. BALON, AND D. L. G. NOAKES. 1979. Distribution, community structure and production of fishes in the upper Speed River, Ontario: a preimpoundment study. Environ. Biol. Fishes 4: 219–244.

MANN, R. H. K., AND C. A. MILLS. 1979. Demographic aspects of fish fecundity. Symp. Zool. Soc. Lond. 44: 161–177.

MATHEWS, W. J., AND J. T. STYRON. 1981. Tolerance of headwater vs. mainstream fishes for abrupt physicochemical changes. Am. Midl. Nat. 105: 149–158.

MILLER, P. J. 1979a. A concept of fish phenology. Symp. Zool. Soc. Lond. 44: 1–28.

1979b. Adaptiveness and implications of small size in teleosts. Symp. Zool. Soc. Lond. 44: 263–296.

MISIK, V. 1959. Ichthyofauna of the Kysuce River. Biol. Pr. 4: 5–40. (In Slovak with German summary)

MOYLE, P. B., AND J. J. CECH JR. 1982. Fishes: an introduction to ichthyology. Prentice Hall, Englewood Cliffs, NJ.

MOYLE, P. B., AND H. W. LI. 1979. Community ecology and predator–prey relations in warmwater streams, p. 171–180. *In* H. Clepper [ed.] Prey–predator systems in fisheries management. Sport Fishing Institute, Washington, DC.

MURPHY, G. I. 1968. Pattern in life history and the environment. Am. Nat. 102: 391–403.

NIKOLSKY, G. V. 1933. On the influence of the rate of flow on the fish fauna of the rivers of central Asia. J. Anim. Ecol. 2: 266–281.

OKOLOWICZ, W. 1977. The climate of Poland, Czechoslovakia, and Hungary, p. 75–125. *In* C. C. Wallén [ed.] Climates of central and southern Europe. World Survey of Climatology. Vol. 6. Elsevier Scientific Publishing Co., New York, NY.

ORIANS, G. H, AND O. T. SOLBRIG. 1977. Degree of convergence of ecosystem characteristics, p. 225–255. *In* G. H. Orians and O. T. Solbrig [ed.] Convergent evolution in warm deserts. Dowden, Hutchinson, and Ross, Stroudsburg.

PASTERNAK, K., AND A. STARJECKA. 1979. Chemism of the River Nida water and some relations between its bacteriological and chemical features. Acta Hydrobiol. 21: 361–395.

PATRICK, R. 1961. A study of the numbers and kinds of species found in rivers in eastern United States. Proc. Acad. Nat. Sci. Phila. 113: 215–258.

1975. Structure of stream communities, p. 445–459. *In* M. L. Cody and J. M. Diamond [ed.] Ecology and evolution of communities. The Belknap Press of Harvard University Press, Cambridge, MA.

PATTERSON, C. 1981. The development of the North American fish fauna — a problem in historical biogeography, p. 265–281. *In* P. L. Forey [ed.] The evolving biosphere. University of Cambridge Press, London.

PATTON, P. C., AND V. R. BAKER. 1976. Morphometry and floods in small drainage basins subject to diverse hydrogeomorphic controls. Water Resour. Res. 12: 941–952.

PAULY, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. J. Cons. Cons. Int. Explor. Mer 39: 175–192.

PENCZAK, T. 1968a. The ichthyofauna of the rivers of the Lodz upland and adjacent areas. Part 1a. The hydrography and fishes of the Bzura River basin. Acta Hydrobiol. 10: 471–497.

1968b. The ichthyofauna of the rivers of the Lodz upland and adjacent areas. Part 1b. The hydrography and fishes of the Pilica River basin. Acta Hydrobiol. 10: 499–524.

1969. The ichthyofauna of the rivers of the Lodz upland and adjacent areas. Part 1c. The hydrography and fishes of the Warta basin. Acta Hydrobiol. 11: 69–118). (In Polish with English summary)

1971. Materials to the knowledge of Nida River basin ichthyofauna. Zesz. Nauk. Univ. Lodzkiego Ser. 2 44: 53–84. (In Polish with English summary)

PERRONE, M. JR., AND T. M. ZARET. 1979. Parental care patterns of fishes. Am. Nat. 113: 351–361.

PFLIEGER, W. L. 1971. A distributional study of Missouri fishes. Univ. Kans. Publ. Mus. Nat. Hist. 20: 225–570.

PIANKA, E. R. 1970. On *r*- and *K*-selection. Am. Nat. 105: 592–597.

PODDUBNYI, A. G. 1979. Ichthyofauna of the Volga, p. 304–339. *In* Ph. D. Mordukhai-Boltovskoi [ed.] The River Volga and its Life. Monogr. Biol. 33. Dr. W. Junk bv Publishers, The Hague.

PUNZET, J. 1969. Hydrological characteristics of the River Raba. Acta Hydrobiol. 11: 423–477.

1976. Hydrological characteristics of the River Skawa and its more important tributaries. Acta Hydrobiol. 18: 353–381.

REGIER, H. A. 1979. A balanced science of renewable resources: with particular reference to fisheries. University of Washington Press, Seattle, WA. 108 p.

REMBISZEWSKI, J. M., AND H. ROLIK. 1975. Cyclostomate et Pisces. Catologus Faunae Poloniae, 38. Panstwowe Wydawnictwo Naukowe, Warsaw. 252 p.

ROBBINS, W. H., AND H. R. MACCRIMMON. 1977. Vital statistics and migratory patterns of a potamodromous stock of smallmouth bass, *Micropterus dolomieui*. J. Fish. Res. Board Can. 34: 142–147.

RODDA, J. C. 1969. The hydrograph, p. 162–175. *In* R. J. Chorley [ed.] Introduction to physical hydrology. Methuen and Co. Ltd., London.

ROFF, D. A. 1981. Reproductive uncertainty and the evolution of iteroparity: why don't flatfish put all their eggs in one basket? Can. J. Fish. Aquat. Sci. 38: 968–977.

ROSENBLATT, R. H. 1963. Some aspects of speciation in marine shore fishes, p. 171–180. *In* J. P. Harding and N. Tebble [ed.] Speciation in the sea. Syst. Assoc. Publ. No. 5, London.

SALE, P. F. 1978. Coexistence of coral reef fishes — a lottery for living space. Environ. Biol. Fishes 3: 85–102.

SCHLOSSER, I. J. 1982. Fish community structure and function along two habitat gradients in a headwater stream. Ecol. Monogr. 52: 359–414.

SCOTT, W. B., AND E. J. CROSSMAN. 1973. Freshwater fishes of Canada. Fish. Res. Board Can. Bull. 184: 966 p.

SEPKOSKI, J. J. JR., AND M. A. REX. 1974. Distribution of freshwater mussels: coastal rivers as biogeographic islands. Syst. Zool. 23: 165–188.

SOROKIN, V. N. 1971. The spawning and spawning grounds of the burbot. J. Ichthyol. 11: 907–915.

STEARNS, S. C. 1976. Life history tactics: a review of the ideas. Quart. Rev. Biol. 51: 3–47.

1977. The evolution of life history traits: a critique of the theory and a review of the data. Annu. Rev. Ecol. Syst. 8: 145–171.

1980. A new view of life-history evolution. Oikos 35: 266–281.

STOTT, B. 1961. Movement of coarse fish in rivers. Nature (London) 190: 737–738.

STRATHMAN, R. R., AND M. F. STRATHMAN. 1982. The relation between adult size and brooding in marine invertebrates. Am. Nat. 119: 91–101.

SVARDSON, G. 1949. Natural selection and egg number in fish. Annu. Rep. Inst. Freshw. Res. Drottningholm 29: 115–122.

SZCZERBOWSKI, J. A. 1972. Fishes in the Lyna River system. Pol. Arch. Hydrobiol. 19: 421–435.

THOMPSON, D. H., AND D. F. HUNT. 1930. The fishes of Champaign County: a study of the distribution and abundance of fishes in small streams. Ill. Nat. Hist. Surv. Bull. 19: 101 p.

TRAMER, E. J. 1977. Catastrophic mortality of stream fishes trapped in shrinking ponds. Am. Midl. Nat. 97: 469–478.

TRAUTMAN, M. B. 1957. The fishes of Ohio, with illustrated keys. Ohio State University Press, Columbus, OH. 683 p.

VANNOTE, R. L., G. W. MINSHALL, K. W. CUMMINS, J. R. SEDELL, AND C. E. CUSHING. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37: 130–137.

WARE, D. M. 1975. Relation between egg size, growth, and natural mortality of larval fish. J. Fish. Res. Board Can. 32: 2503–2512.

WEBB, P. W. 1977. Effects of median-fin amputation on fast-start performance of rainbow trout (*Salmo gairdneri*). J. Exp. Biol. 68: 123–135.

WEINSTEIN, M. P. 1979. Shallow marsh habitats as primary nurseries for fishes and shellfish, Cape Fear River, North Carolina. Fish. Bull. 77: 339–357.

WEINSTEIN, M. P., S. L. WEISS, AND M. F. WALTERS. 1980. Multiple determinants of community structure in shallow marsh habitats, Cape Fear River Estuary, North Carolina, USA. Mar. Biol. 58: 227–243.

WELCOMME, R. L. 1979. Fisheries ecology of floodplain rivers. Longman, London. 317 p.

WHEELER, A. 1969. The fishes of the British Isles and Northwest Europe. Macmillan, London. 613 p.

WILLIAMS, G. C. 1959. Ovary weights of darters: a test of the alleged association of parental care with reduced fecundity in fishes. Copeia 1959: 18–24.

WOOTON, R. J. 1979. Energy cost of egg production and environmental determinants of fecundity in teleost fishes. Symp. Zool. Soc. Lond. 44: 133–159.

ZAR, J. H. 1974. Biostatistical analysis. Prentice-Hall, New York, NY. 620 p.

ZARET, T. M. 1979. Predation in freshwater fish communities, p. 135–143. *In* H. Clepper [ed.] Predator–prey systems in fisheries management. Sport Fishing Institute, Washington, DC.

ZAWISZA, J. 1965. Fisheries in Mazury, p. 53–63. *In* K. Patelas [ed.] Mazury. Part I. Polish Academy of Sciences, Hydrobiological Committee, Krakow.

Contribution of Particulate Phosphorus (> 250 μm) to the Total Phosphorus Pool in Lake Water

E. E. Prepas and J. Vickery

Department of Zoology, University of Alberta, Edmonton, Alta. T6G 2E9

Prepas, E. E., and J. Vickery. 1984. Contribution of particulate phosphorus (> 250 μm) to the total phosphorus pool in lake water. Can. J. Fish. Aquat. Sci. 41: 351–363.

Particulate phosphorus (PP) > 250 μm was concentrated in the euphotic zone of 17 lakes in central Alberta. When the euphotic zone extended below the epilimnion, PP > 250 μm was concentrated deep in the euphotic zone. PP > 250 μm was a significant but variable portion of the total phosphorus (TP) pool in individual lakes; thus, samples should be collected from the euphotic zone on several dates to estimate the contribution of PP > 250 μm to the TP pool. As well, the contribution of this fraction varied among lakes: average summer values for the euphotic zone ranged from 3 to 19%. Among lakes, the contribution of large particles to the TP pool decreased proportionally as lake productivity (estimated by chlorophyll *a* (Chl *a*)) increased. The relative contribution of PP > 250 μm in summer accounted for a significant portion of the residual variation in the spring TP–summer Chl *a* relationship but not the summer TP–summer Chl *a* relationship in the study lakes. These apparently contradictory results can be explained by differences between lakes that mixed intermittently throughout the summer and those that remained permanently thermally stratified during this time.

Le phosphore particulaire (PP) > 250 μm est concentré dans la zone euphotique de 17 lacs du centre de l'Alberta. Quand cette zone se prolonge au-dessous de l'épilimnion, le PP > 250 μm est concentré en profondeur dans la zone euphotique. Le PP > 250 μm représente une portion importante mais variable de la quantité de phosphore (PT) dans les lacs individuels; c'est dire que les échantillons devraient être prélevés dans la zone euphotique à plusieurs dates différentes, afin d'estimer la contribution de PP > 250 μm au pool de PT. De plus, la contribution de cette fraction varie d'un lac à l'autre : les valeurs estivales moyennes dans la zone euphotique sont comprises entre 3 et 19 %. Parmi les lacs, la contribution des grosses particules au pool de PT diminue à mesure qu'augmente la productivité du lac (estimée par chlorophylle *a* (Chl *a*)). La contribution relative de PP > 250 μm en été est responsable d'une portion significative de la variation résiduaire de la relation PT printannier–Chl *a* estivale, mais non de celle de PT estival–Chl *a* estival dans les lacs étudiés. On peut expliquer ces résultats apparemment contradictoires par des différences entre lacs qui se mélangent de façon intermittentes tout au long de l'été et ceux qui demeurent thermiquement stratifiés pendant tout ce temps.

Received July 4, 1983
Accepted November 8, 1983

Reçu le 4 juillet 1983
Accepté le 8 novembre 1983

The literature contains incomplete and conflicting results on the importance of large particles in the phosphorus pool. Dillon and Rigler (1974) found that particles larger than 216 μm constituted only a small portion (average 2%) of the total phosphorus (TP) pool at spring overturn in 19 lakes in central Ontario. Subsequently, Prepas and Rigler (1982) showed that during summer, particulate phosphorus (PP) > 250 μm was an important (12%) and fairly constant fraction of the TP pool in the euphotic zone of Bob Lake (Ontario), a deep oligotrophic lake on the Precambrian Shield. More data are needed on within-and between-lake patterns in this fraction before any general statements can be made about its importance. Lakes with different surface areas, depths, and trophic status ought to be studied. Also, vertical and horizontal patterns in PP > 250 μm need to be established for various lake types. The data could be used to evaluate whether this fraction is required for all lakes sampled for TP and to establish suitable sampling routines.

To evaluate the general contribution of large particles to the phosphorus pool, we collected data on PP > 250 μm over 3 yr in a total of 17 lakes in central Alberta. Samples were collected on several dates and at several depths from each lake. These data were used to (1) evaluate where this fraction was concentrated in the water column, (2) test whether PP > 250 μm was a consistent portion of the TP pool, as reported for Bob Lake, and (3) determine if the relative importance of PP > 250 μm was predictable from an estimate of lake productivity such as chlorophyll *a* (Chl *a*).

Recently, considerable effort has been made to reduce the residual variation in the TP–Chl models (Nicholls and Dillon 1978; Hoyer and Jones 1983). Most TP values in these models either exclude or contain poor estimates of the phosphorus in large particles (Prepas and Rigler 1982). Thus, we used the data collected in this study to test whether including PP > 250 μm and the animal portion of PP > 250 μm reduced the residual variance in the TP–Chl relationship.

Study Lakes

The lakes in this study are situated in glacial till and are located in boreal mixed-wood and lower transition biomes in central Alberta. They are spread out over a large area (7×10^4

km^2) in central Alberta, in the drainage basins of three major river systems (Athabasca, Beaver, and North Saskatchewan rivers). The lakes vary in size (surface areas 0.06–9 km^2), depth (mean 3–19 m), and trophic status (oligotrophic to hypereutrophic). Seventeen lake basins were studied over 3 yr: 8 in 1980, these 8 plus 7 new ones in 1981, and 10 of those studied in 1981 plus 2 new ones in 1982. Baptiste and Amisk lakes both have two distinct basins joined by a channel and are treated as separate lakes. The lakes were divided into two groups based on summer thermal patterns: deep lakes that were permanently thermally stratified and shallow lakes that mixed intermittently. The location and general physical and chemical characteristics of 15 of the study lakes are described in Prepas and Trew (1983).

Materials and Methods

The lakes were sampled from four to seven times from early May until the end of August in 1980, from three to five times from early May until mid-August in 1981, and from six to eight times from mid-May until the end of September in 1982. Each year sampling began within 2 wk of ice melt, which was in the latter part of April in 1980 and 1981 and mid-May in 1982. Vertical profiles of temperature and light at the deepest site were measured on each visit. Temperature was measured at 1-m intervals with a resistance thermometer accurate to 0.1°C; epilimnetic, metalimnetic, and hypolimnetic zones of the water column were defined according to Hutchinson (1957). In 1980 the depth of the euphotic zone was defined as twice the Secchi disk reading and in 1981 and 1982 as 1% surface penetrating irradiance as measured with a Lambda L1-185 light meter with a quantum sensor or a Protomatic photometer.

In all lakes, TP $<$ 250 μm, Chl *a*, and PP $>$ 250 μm levels were determined from pooled samples collected at three to eight stations. The number of stations sampled was proportional to lake surface area and trophic status. Integrated samples for TP $<$ 250 μm and Chl *a* were collected from the epilimnetic and euphotic zones at each station with Tygon tubing, as outlined in Prepas and Trew (1983). PP $>$ 250 μm was sampled with a conical net 90-cm long with a 29-cm-diameter aperture and fitted with a bucket made with 250-μm Nitex mesh. In 1981 and 1982, PP $>$ 250 μm was collected from the euphotic zone in all lakes. To determine the vertical distribution of PP $>$ 250 μm in the deep lakes, samples were collected to three or four depths in 1980 and to two or three depths in 1981. The samples were rinsed with double-distilled water (DDW) (in 1980 and 1981) and lake water (in 1982) into 175-mL Nalgene bottles; hauls taken to the same depth from all stations on the lake were pooled. In 1982, duplicate sets of samples were collected for each lake on each sampling date. On all lakes, samples were also collected from the euphotic zone for plankton identification. These samples were collected with a tow net and preserved in a chilled solution of sugar and formalin (Prepas 1978).

In addition, for the deep lakes, profiles of dissolved oxygen, TP $<$ 250 μm, and Chl *a* were constructed. Water samples were collected for these analyses with a 1.5-L aluminum drop-sleeve water bottle at the deepest site. To determine the depths where dissolved oxygen levels were low, water samples were collected at 1- to 2-m intervals from the middle of the metalimnion to the bottom of the water column or until dissolved oxygen levels reached zero. Because these lakes varied in depth (maximum depth from 15 to 60 m), phosphorus profiles were established from samples collected at 1- to 5-m intervals from the surface to within 2 m of the sediment–water interface. To evaluate the PP $>$ 250 μm–Chl *a* relationship, chlorophyll profiles were constructed from samples collected at 1-m intervals from the surface to the bottom of the euphotic zone at various times in 1981.

To evaluate tow net efficiency, samples collected with the 250-μm tow net on nine lakes in 1981 and 1982 were compared with samples collected with a 40-L Schindler–Patalas Plexiglas trap fitted with a 250-μm Nitex mesh funnel and bucket. The methods of sample collection and calculation are as described in Prepas and Rigler (1982).

The large particles were sampled with a 250-μm net, as Prepas and Rigler (1982) had done. Prepas and Rigler found no difference between PP collected with 80- and 250-μm tow nets fitted with a 250-μm bucket. These results were puzzling; they suggested that PP between 80 and 250 μm was an insignificant portion of the TP pool. To measure PP between 80 and 250 μm, seven duplicate profiles were collected in 1982 from four lakes with a Schindler–Patalas trap fitted with a 250- and 80-μm Nitex net. To determine the relative efficiencies of tow nets made with both sizes of mesh, duplicate sets of tows were taken in the euphotic zone of nine lakes in 1981 and 1982 with nets and buckets made with 250- and 80-μm Nitex mesh. To compare the efficiency of the tow net made with 80-μm mesh in collecting PP and zooplankton (ZP) with the net made with 250-μm mesh, duplicate smples were taken on 15 occasions in 1981 and 1982 with both nets and analyzed for PP and ZP.

Dissolved oxygen was determined by Carpenter's (1965) modified Winkler technique. The ethanol extraction technique was used for determination of Chl *a* (Bergmann and Peters 1980). TP $<$ 250 μm was determined on samples filtered through 250-μm Nitex net and analyzed by Menzel and Corwin's (1965) potassium persulfate method, as modified by Prepas and Rigler (1982). PP $>$ 250 μm and PP $>$ 80 μm were determined on samples that were diluted, subsampled, homogenized, subsampled, and digested with potassium persulfate, as outlined in Prepas and Rigler (1982). TP was calculated as the sum of TP $<$ 250 μm and PP $>$ 250 μm. The containers used for the collection and analysis of samples were washed and rinsed, as outlined in Prepas and Rigler (1982).

To determine the contribution of zooplankton to the large particulate fraction ($>$ 250 μm), the zooplankton $>$ 250 μm were separated out and analyzed for TP in 1982. The samples collected for PP $>$ 250 μm were made up to a known volume (between 100 and 250 mL) with DDW. Three 10-mL subsamples were placed in a 175-mL Nalgene bottle and analyzed for PP $>$ 250 μm, as described previously. The remainder of the sample was rinsed into a graduated cylinder with DDW and made up to a recorded volume (between 100 and 250 mL). To separate the zooplankton from other particles (i.e. phytoplankton) $>$ 250 μm, carbon dioxide was gently bubbled through the sample. In 2–10 min the narcotized zooplankton settled to the bottom of the cylinder, while the phytoplankton remained suspended in the water column (confirmed microscopically). Phosphorus in phytoplankton $>$ 250 μm was determined from three 10-mL subsamples taken from the graduated cylinder and placed in a Nalgene bottle. The remaining water lying over the narcotized zooplankton was then carefully siphoned off leaving the animals concentrated in a small volume of water. The sample (containing only zooplankton) was made up to a recorded volume (50 to 100 mL) with DDW, and three 10-mL subsamples were placed in a Nalgene bottle. These subsamples

were designated the animal portion of the large particulate fraction (ZP > 250 μm) and analyzed for TP following the procedure outlined for PP > 250 μm.

Duplicate samples were collected in 1982 for determination of PP > 250 μm and ZP > 250 μm. The repeatability of the collection and analytical techniques was reasonable; the average standard error of the mean was 10% of the mean concentration for both PP > 250 μm and ZP > 250 μm. The values reported for PP > 250 μm and ZP > 250 μm are the averages of the duplicate samples. When there were large differences (> 50%) between duplicate samples, the fraction phytoplankton > 250 μm was also analyzed for phosphorus as a check on the recorded values.

All regressions were performed on the Amdahl model 580/2 computer at the University of Alberta. Statistical analyses are as outlined in Snedecor and Cochran (1980) and Prepas (1983). Range rather than variance is used as an estimate of dispersion in cases where the sample size is small and the distribution is unknown.

In 1981 and 1982, values for spring TP and mean summer TP and Chl *a* were calculated from samples representing the euphotic zone. In 1981, spring and summer were arbitrarily defined as the months of May and June–August, respectively. Ice melt was very late in 1982. To make the data collected over the 2 yr comparable relative to ice melt, in 1982, spring and summer were defined as 27 May–14 June and 15 June–15 September, respectively. The first samples collected in 1982 were while the ice was breaking up on the lakes.

The composition of the zooplankton communities was remarkably similar in the study lakes. The lakes were dominated by one or two species of cladoceran including at least one *Daphnia* sp. of the *galeata mendotae* or *pulex* groupings, a calanoid copepod, usually *Diaptomus oregonensis* or *D. siciloides*, and one or two cyclopoid copepods, usually from the trio *Cyclops bicuspidatus thomasi*, *C. vernalis*, and *Mesocyclops edax*.

Results

Calibration of Tow Nets

The Schindler–Patalas trap fitted with 250-μm netting collected more PP per unit volume than the 250-μm tow net in 27 of 28 comparisons and more ZP in 20 of 23 comparisons. On average, the Schindler–Patalas trap collected 20% more PP > 250 μm and 20% more ZP > 250 μm than the tow net. The data were quite variable; the ratios of PP > 250 μm and ZP > 250 μm collected by the trap to that collected by the tow net ranged from 0.8 to 2.0 and 0.6 to 2.2, respectively.

We tested whether the distance the net was pulled through the water (Smith et al. 1968) and whether the density of small particles (estimated by summer [Chl *a*]) affected net efficiency and would thus explain some of the variance in our data. The plankton tows were vertical; hence, distance and depths of tow are equivalent. To evaluate the effect of depth on net efficiency, tow net samples were collected to two depths (4 and 8 m, on average) from six lakes. These depths represented the range sampled in most lakes during 1981 and 1982. These tow net samples were calibrated with samples collected over the same depths with a Schindler–Patalas trap (calculations as described in Prepas and Rigler 1982). Over these relatively short distances, tow net efficiency for collecting PP > 250 μm and ZP > 250 μm was not affected by depth of tow (signed-rank tests, $n = 11$ and 7, $P \gg 0.10$). In addition, tow net efficiency was independent of mean summer [Chl *a*] ($r = -0.48$, $n = 9$, $P > 0.10$).

Since tow net efficiency was independent of depth and lake [Chl *a*], all PP (and ZP) values from samples collected with a tow net were increased by 20%. The tow net efficiencies for the Alberta lakes were on average lower than reported for a lake on the Precambrian Shield (Prepas and Rigler 1982).

In addition, the importance of mesh size was evaluated by comparing the contribution of particles between 80 and 250 μm in size and the relative efficiencies of tow nets made with 80- and 250-μm mesh in collecting large particles. The Schindler–Patalas trap fitted with a 250-μm net collected less phosphorus than the trap fitted with an 80-μm net on six of seven occasions: the average ratio for PP was 0.69 (range 0.3–1.2) and for ZP was 0.75 (range 0.5–1.2). Similarly, the 250-μm tow net collected less PP than the 80-μm tow net, but interestingly, more ZP (average ratios 0.76 and 1.1, ranges 0.4–1.3 and 0.8–1.5, respectively). Thus, the large zooplankters were selectively able to avoid the mouth of an 80-μm net (signed-rank test, $n = 15$, $P < 0.01$), possibly because the plume of water above the net mouth was more noticeable with an 80- than a 250-μm net. The 250-μm tow net chosen for this study was equally efficient at collecting large phytoplankton and zooplankton. However, for equal efficiencies with a smaller mesh size, the net design should be modified. These comparisons also demonstrate that the choice of mesh size can affect the relative contribution of PP to the TP pool.

Vertical Distribution of PP > 250 μm

The data collected in 1980 on the deep lakes suggest that PP > 250 μm was largely concentrated in the euphotic zone (Appendix A). Thus, in Amisk N., Amisk S., and Baptiste S. lakes, where the euphotic zone was limited to the epilimnion, PP > 250 μm was also concentrated in the epilimnion throughout most of the sampling period (Fig. 1). However, in Hubbles, Narrow, and Twin lakes where the euphotic zone extended below the epilimnion, concentrations of PP > 250 μm were highest in the epilimnion during spring, and then the maxima descended during summer (Fig. 2). Thus, when the euphotic zone extended below the epilimnion in summer, a PP (> 250 μm) maximum developed in the deeper part of the euphotic zone.

In 1981, we investigated whether the phytoplankton and PP > 250 μm were distributed in similar parts of the water column of deep lakes. Once again, PP > 250 μm was concentrated in the euphotic zone of the study lakes (Fig. 3 and 4). In Amisk N., Amisk S., and Baptiste S. lakes, the euphotic zone was limited to the epilimnion for a 2nd yr. In these lakes, concentrations of Chl *a* and PP > 250 μm were also highest in the epilimnion (Appendix B; Fig. 3). In contrast, in Hubbles, Narrow, Roi, and Sauer lakes the euphotic zone extended into the hypolimnion. In these four lakes, the highest concentrations of Chl *a* and PP > 250 μm were below the epilimnion throughout the summer period (Appendix B; Fig. 4; also included in Appendix B are the incomplete data on three other deep lakes: Eden, Star, and Twin). Thus, in summer in individual lakes, the maximum concentrations of Chl *a* and PP > 250 μm were in the same stratum, although the data are only approximate.

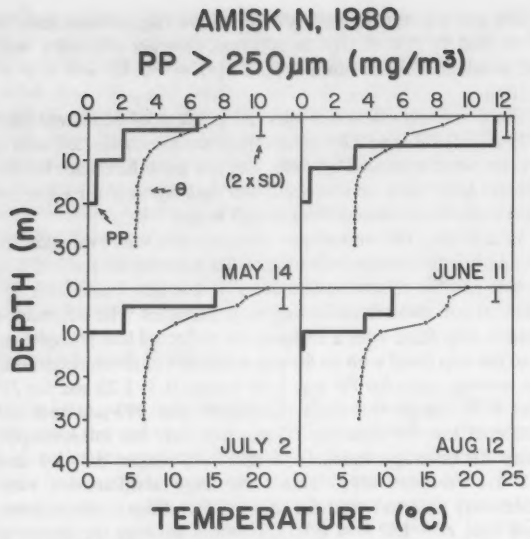


FIG. 1. Vertical distribution of PP > 250 µm and temperature (θ) in Amisk N. Lake, 1980. The approximate depth of the euphotic zone is indicated (2 × SD).

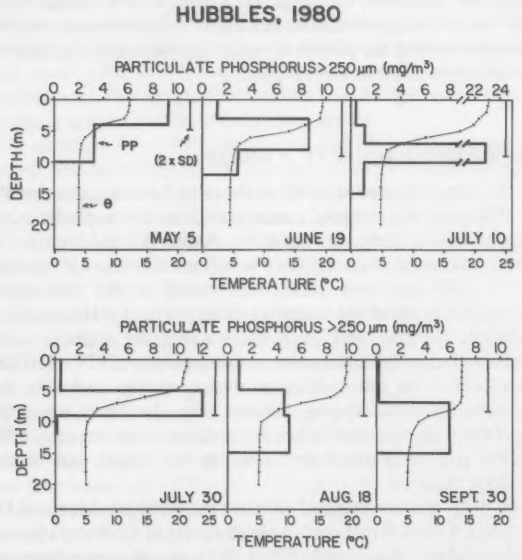


FIG. 2. Vertical distribution of PP > 250 µm and temperature (θ) in Hubbles Lake, 1980. The approximate depth of the euphotic zone is indicated (2 × SD).

Contribution of PP > 250 µm to the TP Pool

In 1981 and 1982, samples were collected to estimate the contribution of PP > 250 µm to the TP pool in the euphotic zone; in 1982, the contribution of ZP > 250 µm to the TP pool in the euphotic zone was also estimated. In the open-water season, the contribution of PP > 250 µm to the TP pool varied as much as 3–31% in Hubbles Lake and 0.4–5% in Nakamun Lake. The temporal patterns were variable, with no clear trends. In the deep lakes studied in 1982 (Table 1) and Eden Lake in 1981, PP > 250 µm was a relatively small portion of the TP

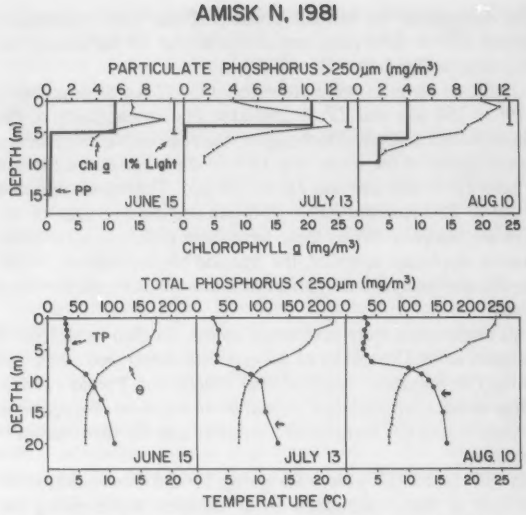


FIG. 3. Vertical distribution of PP > 250 µm, Chl *a*, TP < 250 µm, and temperature (θ) in Amisk N. Lake, 1981. The depth of 1% light is indicated.

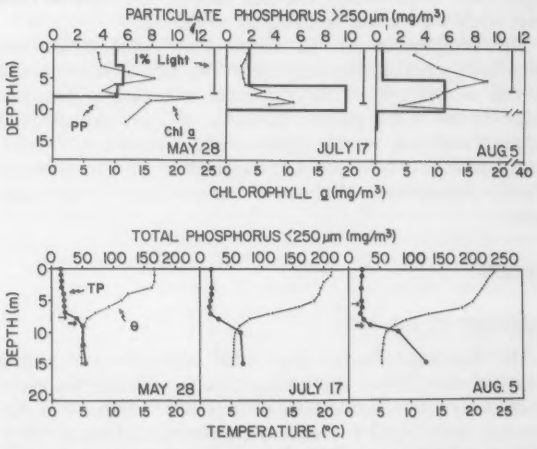


FIG. 4. Vertical distribution of PP > 250 µm, Chl *a*, TP < 250 µm, and temperature (θ) in Hubbles Lake, 1981. The depth of 1% light is indicated.

pool (0–5%) early in the season and then increased to maximum levels (17–23%) in midsummer (Appendices B and C). However, in the other deep lakes studied in 1981 and over all years in the shallow lakes, no consistent patterns emerged (Appendices A, B, and C). Seasonal trends in the contribution of ZP > 250 µm to the TP pool were similar to PP > 250 µm in most lakes (Appendix C). The seasonal changes in PP > 250 µm and ZP > 250 µm were apparently independent of changes in either TP < 250 µm or Chl *a* levels (Fig. 5).

In individual deep lakes, PP > 250 µm varied as much as 6–20% of the TP pool in the euphotic zone (Appendices B and C). In the shallow lakes, the contribution of PP > 250 µm in the euphotic zone in summer varied from 8–26% in Nakamum in 1981 to 1–7% in Wizard in 1982 (Appendices B and C). Thus,

TABLE 1. Average summer (euphotic zone) values for particulate phosph
pool in these fractions in the euphotic zone of the 17 lakes in central Alberta
μm, average summer TP, and average summer Chl *a* values for the eup
thermally stratified (deep) and those that mixed intermittently (shallow).

	% PP > 250 μm / TP	% ZP > 250 μm / TP	Avg. summer PP > 250 μm (mg/m^3)	A Z
Deep lakes				
Amisk N.	16.7	—	6.6	
	16.2	12.4	6.8	
Amisk S.	15.5	—	5.9	
	17.0	11.5	7.1	
Baptiste S.	9.8	—	4.1	
	17.5	15.4	7.4	
Eden	11.0	—	2.7	
	16.8	14.4	3.7	
Hubbles	16.9	—	4.8	
	—	—	—	
Narrow	8.1	—	1.1	
	—	—	—	
Peanut	—	—	—	
	16.0	13.4	4.2	
Roi	12.7	—	2.1	
	—	—	—	
Sauer	6.0	—	2.6	
	15.0	12.0	4.3	
Star	18.9	—	5.0	
	—	—	—	
Twin	14.4	—	2.2	
	19.3	15.0	2.5	
Shallow lakes				
Baptiste N.	10.4	—	3.9	
	9.3	7.8	6.5	
Lessard	—	—	—	
	15.4	8.7	5.1	
Mink	18.4	—	5.9	
	8.9	6.2	5.0	
Nakamun	3.1	—	5.1	
	—	—	—	
Wizard	10.9	—	4.2	
	3.3	2.4	1.7	
Unclassified				
Hasse	15.5	—	3.9	
	14.6	10.7	3.7	

e phosphorus in the fractions > 250 μm (PP > 250 μm and ZP > 250 μm) and percent of the TP
l Alberta sampled in 1981 and 1982. Spring TP < 250 μm, spring TP, average summer TP < 250
the euphotic zone are also presented. The lakes are divided into those that were permanently
hallow). Data are in chronological order.

ner μm	Avg. summer ZP > 250 μm (mg/m^3)	Spring TP < 250 μm (mg/m^3)	Spring TP (mg/m^3)	Summer TP < 250 μm (mg/m^3)	Summer TP (mg/m^3)	Summer Chl *a* (mg/m^3)
	—	—	—	31.6	38.2	18.3
	5.1	57.4	62.7	31.9	38.7	10.6
	—	—	—	33.0	38.9	20.7
	4.7	55.0	60.3	32.1	39.2	15.3
	—	—	—	38.0	42.1	26.0
	6.5	53.0	53.3	36.6	44.0	14.0
	—	28.7	29.4	19.6	22.3	9.2
	3.1	26.6	27.9	18.1	21.8	3.3
	—	26.2	32.0	20.7	25.5	7.6
	—	—	—	—	—	—
	—	11.1	13.3	11.8	12.9	3.4
	—	—	—	—	—	—
	—	—	—	—	—	—
	3.4	30.9	32.5	21.8	26.0	4.6
	—	13.4	31.6	14.8	16.9	5.8
	—	—	—	—	—	—
	—	33.0	34.2	31.7	34.3	18.6
	3.3	36.6	37.9	23.8	28.1	3.8
	—	28.8	32.8	21.2	26.2	5.4
	—	—	—	—	—	—
	—	16.3	18.4	12.8	15.0	2.3
	1.9	13.3	16.3	10.6	13.1	1.2
	—	—	—	46.2	50.1	34.8
	5.6	47.8	49.4	63.8	70.3	18.2
	—	—	—	—	—	—
	2.9	28.7	35.1	25.2	30.3	13.0
	—	24.7	32.3	26.9	32.8	5.3
	3.5	32.0	35.9	46.7	51.7	14.3
	—	78.4	78.7	155	160	150
	—	—	—	—	—	—
	—	36.3	46.1	44.2	48.4	26.4
	1.2	35.4	39.2	54.8	56.5	18.8
	—	27.0	34.0	21.4	25.3	3.3
	2.7	31.9	33.2	22.2	25.9	3.8

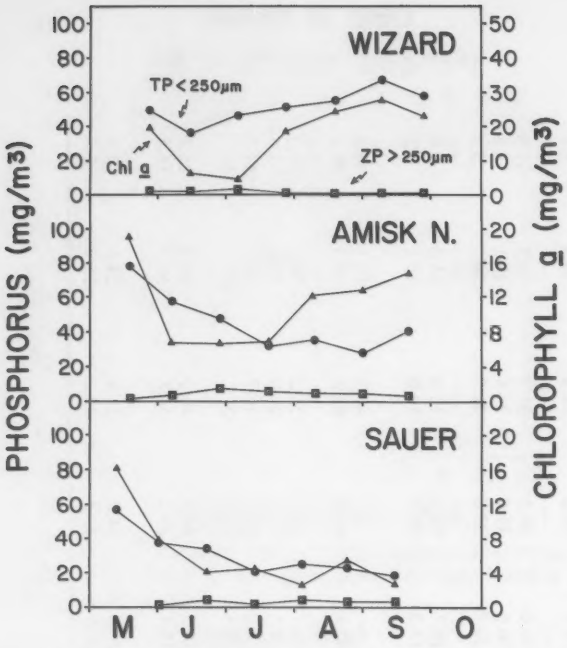


FIG. 5. Temporal variation in the concentration of TP < 250 µm, Chl *a*, and particulate phosphorus in zooplankton (ZP) > 250 µm in three lakes in central Alberta in 1982.

to estimate the contribution of PP > 250 µm to the summer TP pool, samples should be collected over several dates.

In individual lakes, the average summer contribution of PP > 250 µm to the TP pool in the euphotic zone varied from 3 to 19% (Table 1). This ratio also varied for individual lakes from year to year. In deep lakes, PP > 250 µm averaged 15% (±0.9; $\bar{X}$ ± SE) of the TP pool, whereas in shallow lakes it averaged 10% (±1.9) (Table 1). The mean values for deep and shallow lakes are significantly different (Wilcoxon test, $n_1 = 8$, $n_2 = 17$, $P < 0.05$). This difference between deep and shallow lakes was even clearer in the animal fraction: in the deep lakes ZP > 250 µm was 12–15% (13 ± 0.5) of the TP pool, whereas in the shallow lakes it was 2–9% (6 ± 1.4) of the TP pool (Table 1). The animal fraction was a major portion of PP > 250 µm; ZP > 250 µm averaged 76% of PP > 250 µm, 80% in deep lakes, and 71% in shallow lakes. Thus, both PP > 250 µm and ZP > 250 µm tended to be a larger portion of the TP pool in deep as compared with shallow lakes.

PP > 250 µm–Chl Relationsip

Also tested was the possibility of significant relationships between mean summer Chl *a*, as an estimate of lake productivity, and either absolute or relative amounts of PP > 250 µm and ZP > 250 µm (Table 1). The fraction of the TP pool incorporated in PP > 250 µm was negatively correlated with [Chl *a*] ($r = -0.52$, $n = 27$, $P < 0.01$) and with the fraction of the TP pool incorporated in ZP > 250 µm ($r = -0.67$, $n = 12$, $P = 0.02$). The concentrations of PP > 250 µm and ZP > 250 µm were not significantly related to [Chl *a*], although these relationships were positive, rather than negative ($r = 0.15$, $n = 27$, $P = 0.47$; $r = 0.36$, $n = 12$, $P = 0.25$, respectively). Thus, the relative contribution of large particles (PP > 250 µm and ZP > 250 µm) to the TP pool decreased as [Chl *a*] increased.

PP > 250 µm and the TP–Chl Relationship

If the TP pool is partitioned between plant and animal biomass, then in lakes where the phytoplankton biomass is larger than predicted from the TP pool, the zooplankton biomass should be smaller, and vice versa. Partitioning of the TP pool between standing stocks of algae and large zooplankton has been suggested as a possible explanation for much of the residual variation in the TP–Chl models (Harris 1980). This hypothesis was tested with data collected on spring TP < 250 µm and average summer TP < 250 µm, Chl *a*, and contribution of large zooplankton to the TP pool. The average summer contribution of large zooplankton to the TP pool was estimated by the percent of TP in PP > 250 µm in 1981 and percent of TP in ZP > 250 µm in 1982 (Table 1). Because ZP > 250 µm was only measured in 1982, separate comparisons were made for data collected in the 2 yr.

The sample sizes (15 in 1981 and 12 in 1982) were too small to use a multiple regression of Chl *a* on TP < 250 µm and PP > 250 µm or ZP > 250 µm. To estimate the contribution of large zooplankton to the residual variation in the TP–Chl models, an approach appropriate for small samples was chosen. Independent TP–Chl models were used to predict ($\log_{10}$) mean summer [Chl *a*] from concentrations of TP < 250 µm measured in either spring or summer. Deviations of the predicted and the observed Chl values were compared with the fraction of the TP pool tied up in PP or ZP > 250 µm. To predict mean summer [Chl *a*], Dillon and Rigler's (1974) model was used with spring TP values measured in 1981:

$$(1)\quad \log_{10}[\text{Chl } a] = -1.136 + 1.449 \log_{10}[\text{TP}]_{sp}.$$

Jones and Bachmann's (1976) model was used with summer TP values measured in 1981:

$$(2)\quad \log_{10}[\text{Chl } a] = -1.09 + 1.46 \log_{10}[\text{TP}]_{su}.$$

Prepas and Trew's (1983) models (based on data collected from Alberta lakes in 1980 and 1981) were used with both spring and summer TP values in 1982:

$$(3)\quad \log_{10}[\text{Chl } a] = -0.676 + 1.119 \log_{10}[\text{TP}]_{sp}$$

and

$$(4)\quad \log_{10}[\text{Chl } a] = -0.661 + 1.146 \log_{10}[\text{TP}]_{su}.$$

$[\text{TP}]_{sp}$ and $[\text{TP}]_{su}$ refer to concentrations of TP < 250 µm in spring and summer, respectively. Equations 3 and 4 were not used with the 1981 data because they are based in part on these same data.

In both years, the fraction of TP in the large zooplankton was correlated with the deviations of the predicted [Chl *a*] based on the spring values of TP < 250 µm, from the observed [Chl *a*] (eq. 1 and 3). In 1981, 58% of the variation in the spring TP–summer Chl relationship was accounted for by the relative contribution of PP > 250 µm to the TP pool ($r^2 = 0.58$, $n = 15$, $P < 0.01$) (Fig. 6). Similarly, in 1982, 64% of the variation in the spring TP–summer Chl relationship was accounted for by the relative contribution of ZP > 250 µm to the TP pool ($r^2 = 0.64$, $n = 12$, $P < 0.01$) (Fig. 7). However, the fraction of TP in the large zooplankton was not correlated with the deviations of the predicted [Chl *a*], based on the summer values (eq. 2 and 4) of TP < 250 µm, from the observed [Chl *a*] ($r^2 = 0.15$, $n = 15$, $P = 0.15$ for 1981; $r^2 = 0.08$, $n = 12$, $P = 0.38$ for 1982).

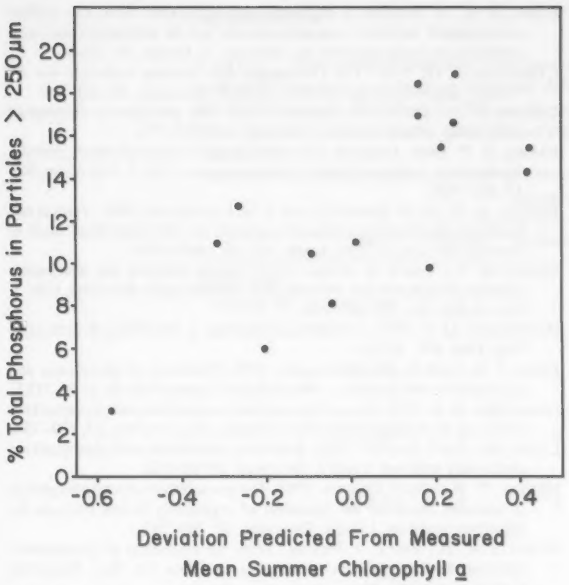


FIG. 6. Relationship between percent of the TP pool in PP > 250 µm and the deviations of the predicted [Chl *a*] based on spring concentration of TP < 250 µm and observed mean summer [Chl *a*] in 15 lakes in 1981.

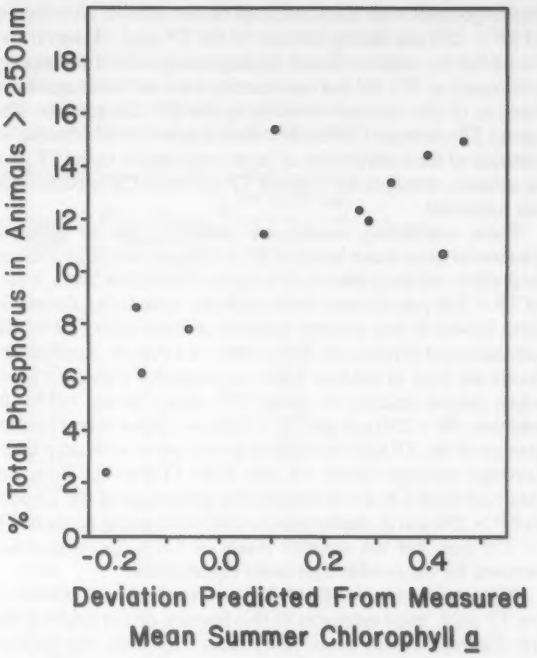


FIG. 7. Relationship between percent of the TP pool in the animal portion of PP > 250 µm and the deviations of the predicted [Chl *a*] based on spring concentration of TP < 250 µm and observed mean summer [Chl *a*] in 12 lakes in 1982.

Thus, the fraction of the TP pool in the large zooplankton explained a significant amount of the variation in the spring TP–summer Chl models, but not in the summer TP–summer Chl models.

Phosphorus–Chl models are based on TP < 250 µm. Since PP > 250 µm accounted for a significant fraction of the TP pool (Table 1), we investigated whether including PP > 250 µm in the TP–Chl relationship would improve the relationship. Neither the spring TP–summer Chl ($n = 23$, $r = 0.74$ and 0.78 for TP < 250 µm and TP, respectively) nor the summer TP–summer Chl ($n = 27$, $r = 0.90$ and 0.89 for TP < 250 µm and TP, respectively) relationship improved substantially when the corresponding PP > 250 µm was included in TP (Table 1).

Discussion

In this study, PP > 250 µm was an important part of the TP pool in the euphotic zone in summer (average 13%, Table 1) but decreased to undetectable levels below this zone. Prepas and Rigler (1982) reported similar results for Bob Lake, a lake on the Precambrian Shield. However, contrary to the Bob Lake study, in this study the relative importance of PP > 250 µm varied by as much as sevenfold over a summer in individual lakes. Also, contrary to the previous study, PP > 250 µm tended to aggregate below the epilimnion when the euphotic zone was relatively deep.

An explanation for the differences in the vertical distribution of PP > 250 µm in Bob Lake and lakes such as Hubbles (Fig. 2 and 4) lies in the chemical conditions in the hypolimnia of the two lake types. The hypolimnion of Bob Lake was well oxygenated, and TP levels were only slightly higher in the hypolimnion than in the epilimnion (Prepas and Rigler 1982). However, most deep lakes in central Alberta are partially meromictic. In these lakes, dissolved oxygen levels are low in the hypolimnion and concentrations of TP < 250 µm are often severalfold higher in the hypolimnion than in the epilimnion. In some of these lakes, the phytoplankton (estimated by Chl *a*) aggregate below the epilimnion (Prepas and Trew 1983).

The results of this study have important implications for sampling programs designed to estimate PP > 250 µm for an entire lake: (1) to estimate the contribution of large particles to the TP pool, PP > 250 µm should be sampled throughout the study period and (2) PP > 250 µm should be estimated from the euphotic zone rather than from surface water samples.

In this study, the vertical distribution of PP > 250 µm and Chl *a* were alike in summer (Appendix B; Fig. 3 and 4). Similarly, the vertical distributions of the zooplankton and phytoplankton biomasses are often alike (Schindler and Novén 1971; Longhurst 1976; Herman et al. 1981). Our results probably apply outside the study area because the majority of PP > 250 µm was large zooplankton and Chl *a* is an estimate of phytoplankton biomass.

The average summer concentrations of PP > 250 µm and ZP > 250 µm were not correlated with mean summer [Chl *a*]. However, the percentages of the TP pool in PP > 250 µm or ZP > 250 µm were negatively correlated with [Chl *a*]. These results are in agreement with the idea (Harris 1980) that the TP pool is partitioned between the standing stocks of algae and large zooplankton.

There are suggestions that the large zooplankton can regulate the size of the phytoplankton community (Shapiro et al. 1975; Bürgi et al. 1979; Lynch and Shapiro 1981; Hoyer and Jones 1983). These observations prompted Harris (1980) to postulate that some of the residual variation in the TP–Chl models is due to the relative size of the zooplankton community. We tested

this hypothesis with data collected on the relative contribution of PP > 250 μm during summer to the TP pool. However, we found that the relative size of the large zooplankton community (estimated as PP) did not consistently account for a significant fraction of the residual variation in the TP–Chl models. The spring TP–summer Chl models were improved by including an estimate of the contribution of large zooplankton to the TP pool in summer, whereas the summer TP–summer Chl models were not improved.

These conflicting results are probably due to different patterns in open-water levels of TP < 250 μm and PP > 250 μm in shallow and deep lakes in this region. In shallow lakes, levels of TP < 250 μm increase in the euphotic zone during the period from ice-out to late summer whereas in deep lakes, TP < 250 μm decreases (Prepas and Trew 1983). As a result, summer Chl levels are high in shallow lakes as compared with deep lakes when judged relative to spring TP values (Riley 1983). In addition, PP > 250 μm and ZP > 250 μm tended to be a smaller portion of the TP pool in shallow as compared with deep lakes (average summer values 15 and 10%) (Table 1). Thus, the relatively high Chl levels and the low percentage of the TP pool in PP > 250 μm in shallow lakes relative to spring levels of TP < 250 μm, but not summer levels of TP < 250 μm, could account for the conflicting results reported here.

Although the fraction PP > 250 μm is a significant portion of the TP pool, good estimates of this fraction do not improve the TP–Chl relationship in our study lakes. However, this fraction is important when considering seasonal variation in the TP pool (e.g. Prepas and Rigler 1981).

Acknowledgments

We thank D. Bird, G. Hutchinson, K. Luco, L. Jorgenson, and I. Wisheu for their assistance with collection and analysis of samples, W. M. Chamberlain, H. J. Fricker, and C. J. Strobeck for reviewing the manuscript, and the Natural Sciences and Engineering Research Council of Canada, the Research Management Division of Alberta Environment, and the Alberta Environment Research Trust for financial support in the form of an operating grant, grant, and contract, respectively, to E. E. Prepas.

References

BERGMANN, M., AND R. H. PETERS. 1980. A simple reflectance method for the measurement of particulate pigment in lakewater and its application to phosphorus–chlorophyll–seston relationships. Can. J. Fish. Aquat. Sci. 37: 111–114.

BÜRGI, H. R., H. BÜHRER, J. BLOESCH, AND E. SZABO. 1979. Der einfluss experimentell variierter zooplanktondichte auf die produktion und sedimentation im hocheutrophen see. Schweiz. Z. Hydrol. 41: 38–63.

CARPENTER, J. H. 1965. The Chesapeake Bay Institute technique for the Winkler dissolved oxygen method. Limnol. Oceanogr. 10: 141–143.

DILLON, P. J., AND F. H. RIGLER. 1974. The phosphorus–chlorophyll relationship in lakes. Limnol. Oceanogr. 19: 767–773.

HARRIS, G. P. 1980. Temporal and spatial scales in phytoplankton ecology. Mechanisms, methods, models, and management. Can. J. Fish Aquat. Sci. 37: 877–900.

HERMAN, A. W., D. D. SAMEOTO, AND A. R. LONGHURST. 1981. Vertical and horizontal distribution patterns of copepods near the shelf break south of Nova Scotia. Can. J. Fish. Aquat. Sci. 38: 1065–1076.

HOYER, M. V., AND J. R. JONES. 1983. Factors affecting the relationship between phosphorus and chlorophyll *a* in midwestern reservoirs. Can. J. Fish. Aquat. Sci. 40: 192–199.

HUTCHINSON, G. E. 1957. A treatise on limnology. I. John Wiley & Sons Ltd., New York, NY. 1015 p.

JONES, J. R., AND R. W. BACHMANN. 1976. Prediction of phosphorus and chlorophyll levels in lakes. J. Water Pollut. Control Fed. 48: 2176–2182.

LONGHURST, A. R. 1976. Interactions between zooplankton and phytoplankton profiles in the eastern tropical Pacific Ocean. Deep-Sea Res. 23: 729–754.

LYNCH, M., AND J. SHAPIRO. 1981. Predation, enrichment, and phytoplankton community structure. Limnol. Oceanogr. 26: 86–102.

MENZEL, D. W., AND N. CORWIN. 1965. The measurement of total phosphorus in seawater based on the liberation of organically bound fractions by persulfate oxidation. Limnol. Oceanogr. 10: 280–282.

NICHOLLS, K. H., AND P. J. DILLON. 1978. An evaluation of phosphorus–chlorophyll–phytoplankton relationship for lakes. Int. Rev. Gesamten Hydrobiol. 63: 141–154.

PREPAS, E. 1978. Sugar-coated *Daphnia*: an improved fixation technique for Cladocera. Limnol. Oceanogr. 23: 557–559.

PREPAS, E. E. 1983. Some statistical methods for the design of experiments and analysis of samples, p. 266–335. *In* J. A. Downing and F. H. Rigler [ed.] A manual on methods for the assessment of secondary productivity in freshwaters. Blackwell Scientific Publications, London.

PREPAS, E. E., AND F. H. RIGLER. 1981. A test of a simple model to predict short-term changes in the phosphorus concentration in lake water. Verh. Int. Ver. Limnol. 21: 187–196.

1982. Improvements in quantifying the phosphorus concentration in lake water. Can. J. Fish. Aquat. Sci. 39: 822–829.

PREPAS, E. E., AND D. O. TREW. 1983. Evaluation of the phosphorus–chlorophyll relationship for lakes off the Precambrian Shield in western Canada. Can. J. Fish. Aquat. Sci. 40: 27–35.

RILEY, E. T. 1983. Internal phosphorus loading from the sediments and the phosphorus–chlorophyll model in shallow lakes. M.Sc. thesis, University of Alberta, Edmonton, Alta. 94 p.

SCHINDLER, D. W., AND B. NOVÉN. 1971. Vertical distribution and seasonal abundance of zooplankton in two shallow lakes of the Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Board Can. 28: 245–256.

SHAPIRO, J., V. LAMARRA, AND M. LYNCH. 1975. Biomanipulation: an ecosystem approach to lake restoration, p. 85–96. *In* P. L. Brezonik and J. L. Fox [ed.] Proc. Symp. Water Qual. Manage. through Biol. Control. University of Florida Press, Gainesville, FL.

SMITH, P. E., R. C. COUNTS, AND R. I. CLUTTER. 1968. Changes in filtering efficiency of plankton nets due to clogging under tow. J. Cons. Cons. Int. Explor. Mer 32: 232–248.

SNEDECOR, G. W., AND W. G. COCHRAN. 1980. Statistical methods. 7th ed. Iowa State University Press, Ames, IA. 507 p.

Appendix A

TABLE A. Particulate phosphorus in the fraction > 250 μm (PP > 250 μm) and percent of the TP pool in this fraction in eight lakes in central Alberta studied in 1980. The depths of the mixed and the euphotic zones, and where the PP samples were collected, are given. The lakes are divided into those that were permanently thermally stratified (deep) and those that mixed intermittently (shallow).

		Depth (m)			PP > 250 μm	% PP > 250 μm
	Date	Mixed	Euphotic	Sample	(mg/m^3)	TP
Deep lakes						
Amisk N.	14 May	3	4	0–3	6.4	8.8
				3–10	2.0	2.4
				10–20	0.4	0.4
	11 June	7	5	0–7	11.4	20.3
				7–12	3.2	3.5
				12–20	0.6	0.4
	2 July	4	4	0–4	7.5	18.9
				4–10	2.1	3.7
				10–15	0	0
	22 July	4	3	0–4	8.7	19.0
				4–10	3.7	6.6
				10–15	2.0	1.3
	12 Aug.	6	3	0–6	5.4	14.0
				6–10	3.8	8.6
				10–15	0	0
Amisk S.	14 May	3	4	0–3	9.7	12.3
				3–10	3.0	3.4
				10–20	0	0
	11 June	6	4	0–6	12.4	22.7
				6–11	5.8	8.2
				11–20	0	0
	2 July	4	4	0–4	7.2	17.4
				4–10	3.1	6.1
				10–15	1.7	1.4
	22 July	6	3	0–3	3.2	8.4
				3–9	6.7	8.7
				9–15	0.8	0.7
	12 Aug.	5	3	0–5	6.7	16.5
				5–10	6.4	10.6
				10–15	0	0
Baptiste S.	13 May	3	3	0–3	1.3	1.7
				3–6	0.3	0.3
				6–15	1.5	1.2
	10 June	8	4	0–8	3.6	7.2
				8–12	1.3	1.3
				12–15	0	0
	3 July	6	3	0–6	7.1	15.2
				6–15	0.7	0.5
	23 July	4	3	0–4	11.3	19.8
				4–9	5.5	7.6
				9–15	1.1	0.5
	13 Aug.	6	2	0–8	4.3	6.6
				8–11	8.2	7.0
				11–15	1.3	0.6
Hubbles	5 May	3	5	0–4	9.2	25.4
				4–10	3.2	1.7
	19 June	3	9	0–3	1.2	6.8
				3–8	8.6	39.6
				8–12	2.9	5.4
	10 July	5	9	0–4	0.4	2.6
				4–7	1.1	5.6
				7–10	22.9	33.5
				10–15	0	0
	30 July	5	9	0–5	0.5	2.6
				5–9	12.1	17.4
				9–12	0	0

TABLE A. (*Concluded*)

	Date	Depth (m) Mixed	Euphotic	Sample	PP > 250 μm (mg/m³)	% PP > 250 μm TP
	18 Aug.	5	10	0–5	0.9	5.4
				5–9	4.6	11.9
				9–15	5.0	7.7
	30 Sept.	7	10	0–7	0.4	2.2
				7–15	6.0	14.1
Narrow	16 June	4	12	0–4	0.1	0.4
				4–9	3.6	21.3
				9–18	2.4	16.3
	7 July	4	10	0–4	0.7	4.7
				4–10	2.6	15.0
	28 July	5	11	0–5	0.7	5.5
				5–10	3.6	19.6
				10–15	3.8	21.8
				15–20	0	0
	20 Aug.	6	13	0–6	0.2	2.3
				6–9	2.0	14.0
				9–15	4.3	21.8
Twin	8 May	5	6	0–5	2.0	9.8
				5–8	1.2	4.3
				8–15	0	0
	23 May	4	10	0–10	0.9	6.6
	5 June	6	9	0–6	4.5	23.5
				6–9	3.4	16.6
				9–15	0.2	0.6
	24 June	6	6	0–3	2.4	13.6
				3–9	1.0	9.1
				9–20	0.4	1.0
	15 July	3	9	0–3	0.1	0.6
				3–8	1.8	16.4
				8–15	2.5	8.8
	7 Aug.	5	8	0–5	0.3	3.4
				5–10	1.7	16.9
				10–15	2.7	8.2
	25 Aug.	5	10	0–5	2.1	18.1
				5–10	0.7	7.7
				10–15	1.2	3.2
Shallow lakes						
Baptiste N.	13 May	3	4	0–3	1.1	2.0
	10 June	3	4	0–4	7.6	14.5
	3 July	—	3	0–4	8.1	14.4
	23 July	—	2	0–4	12.6	13.7
	13 Aug.	5	2	0–4	8.0	8.7
Nakamun	12 May	5	8	0–5	18.6	27.9
	19 June	3	4	0–5	28.9	22.6
	10 July	4	2	0–4	39.5	23.9
	30 July	5	2	0–5	19.5	8.2
	18 Aug.	4	2	0–4	5.6	2.9

Appendix B

TABLE B. Particulate phosphorus in the fraction > 250 μm (PP > 250 μm) and percent of the TP pool in this fraction in the euphotic zone of the 15 lakes in central Alberta studied in 1981. Depths where chlorophyll maximum (Chl_{max}) and PP > 250 μm maximum (PP_{max}) were measured and depths of the mixed and the euphotic zones are indicated. The lakes are divided into those that were permanently thermally stratified (deep) and those that mixed intermittently (shallow).

		Depth (m)				PP > 250 μm	% PP > 250 μm
	Date	Chl_{max}	PP_{max}	Mixed	Euphotic	(mg/m^3)	TP
Deep lakes							
Amisk N.	15 June	3	0–5	5	5	5.5	14.8
	13 July	4	0–4	5	4	10.4	23.8
	10 Aug.	1	0–3	3	3	4.0	11.4
Amisk S.	15 June	3–6	0–6	6	6	5.1	14.8
	13 July	4–6	4–6	6	4	7.6	19.2
	10 Aug.	0–4	0–4	4	4	5.1	12.6
Baptiste S.	16 June	1	0–3	3	6	2.1	6.3
	14 July	0	0–3	6	3	9.1	20.3
	11 Aug.	2	0–2	4	2	1.2	2.8
Eden	6 May	2–6	0–2	4	6	0.7	2.4
	3 June	7	0–5	2	8	1.7	6.6
	6 July	11	—	4	9	2.6	7.1
	21 July	10	—	4	6	3.8	19.4
Hubbles	4 May	—	6–8	4	8	6.3	15.6
	28 May	3, 8	3–6	3	8	5.3	19.6
	24 June	—	6–8.5	5	8.5	9.4	31.1
	17 July	7, 8.5	6–10	5	9	4.4	16.9
	5 Aug.	5, 10	5–10	5	6	0.6[b]	2.8[b]
Narrow	19 May	10–15[a]	0–6	6	15	2.2	14.3
	10 June	4–11[a]	4–15	4	11	1.9	13.9
	27 July	10[a]	15–20	5	12	0.3[b]	2.3[b]
Roi	7 May	4–8	0–4	4	8	0.7	4.8
	9 June	3–8	4–8	3	8	3.3	19.4
	30 June	9	4–7	4	7	1.8	11.9
	29 July	8	4–9	4	9	1.2	6.6
Sauer	7 May	0–4	0–4	4	4	1.2	3.5
	9 June	3–7	3–7	4	7	2.7	6.9
	30 June	4–7	4–8	4	8	3.2	7.1
	29 July	7	0–4	4	7	2.0	3.9
Star	5 May	4–5.5	—	4	5.5	4.0	12.1
	1 June	4–5	—	4	5	4.1	16.3
	23 June	0–5	—	4	5	6.2	20.9
	20 July	0–4	—	4	4	4.6	19.5
Twin	11 May	5–9	0–5	5	9	2.1	11.6
	8 June	5–9	0–5	3	11	2.3	14.8
	1 July	0–12	0–4	4	12	2.0	14.0
Shallow lakes							
Baptiste N.	16 June	0–5	0–3	3	5	2.3	14.7
	14 July	5–10	—	5	5	6.9	12.6
	11 Aug.	0–2	0–2	5	2	2.4	4.0
Mink	5 May	0–5	—	7	5	7.6	23.4
	1 June	—	—	5	5	8.2	26.1
	23 July	—	—	7	5	2.8	21.1
	20 July	0–5	Uniform	4	5	6.8	8.1
Nakamun	20 May	—	—	7	4	0.3	0.4
	10 June	—	—	7	1.5	0.7	0.7
	22 June	0–1.2	0–1.2	6	1.2	7.5	3.6
	21 July	0–0.6	0–0.6	2	0.6	4.7	2.7
	5 Aug.	0–1	0–1	6	1	7.4	5.3
Wizard	2 June	0–5	—	7	5	9.8	27.7
	1 July	0–5	0–5	7	5	4.0	11.1
	28 July	0–2.5	—	9	2.5	1.2	2.0
	12 Aug.	0–2	—	3	2	1.7	2.8

TABLE B. (*Concluded*)

	Date	Depth (m)				PP > 250 μm (mg/m³)	% PP > 250 μm / TP
		Chl_{max}	PP_{max}	Mixed	Euphotic		
Unclassified							
Hasse	6 May	2–5	2–5	7	5	7.0	20.6
	3 June	—	—	8	8	4.5	18.5
	24 June	4–8	0–4	8	8	2.9	11.4
	22 July	2–8	3–8	4	8	4.3	16.5

[a]Maximum depth measured.
[b]These low values are likely a function of how the euphotic zone was defined.

Appendix C

TABLE C. Particulate phosphorus in the fractions > 250 μm (PP > 250 μm and ZP > 250 μm) and percent of the TP pool in these fractions in the euphotic zone of the 12 lakes in central Alberta studied in 1982. The lakes are divided into those that were permanently thermally stratified (deep) and those that mixed intermittently (shallow).

	Date	Depth (m)	PP > 250 μm (mg/m³)	ZP > 250 μm (mg/m³)	% PP > 250 μm / TP	% ZP > 250 μm / TP
Deep lakes						
Amisk N.	17 May	5	1.3	1.1	1.7	1.4
	6 June	8	5.3	3.3	8.5	5.3
	27 June	7	7.4	4.6	13.7	8.9
	19 July	5	7.7	6.4	19.3	16.1
	9 Aug.	4	6.2	4.7	14.8	11.2
	31 Aug.	7	5.8	4.5	17.1	13.5
	20 Sept.	4	5.1	3.2	11.0	7.0
Amisk S.	17 May	6	1.7	1.5	2.0	1.8
	7 June	7	5.3	2.9	8.8	4.8
	28 June	6	6.7	4.2	13.6	8.4
	19 July	5	6.0	5.3	17.0	14.9
	9 Aug.	4.5	9.2	5.7	19.6	12.2
	31 Aug.	7	6.4	3.8	17.9	10.5
	20 Sept.	5	3.1	2.3	7.2	5.3
Baptiste S.	18 May	4	0.5	0.2	0.4	0.2
	8 June	6	0.3	0.2	0.5	0.4
	28 June	4	2.7	1.9	5.1	3.7
	20 July	6	9.2	7.6	23.2	19.2
	10 Aug.	3.5	10.8	9.3	22.5	19.3
	1 Sept.	5	7.1	7.2	19.2	19.4
	21 Sept.	6	4.1	3.9	8.8	8.4
Eden	12 May	6	0.2	—	0.4	—
	1 June	8	1.3	0.8	4.7	3.0
	22 June	8	4.4	2.8	18.5	12.0
	13 July	9	3.7	2.7	16.3	12.0
	4 Aug.	7.5	4.4	3.9	18.6	16.4
	23 Aug.	8	3.3	3.7	15.8	17.7
	14 Sept.	8	2.6	2.5	14.7	14.1
Peanut	25 May	8	0.2	0.1	0.5	0.4
	9 June	8	1.6	1.1	4.8	3.3
	21 June	9	5.3	4.0	16.6	12.5
	3 Aug.	8	3.4	2.8	13.6	11.3
	24 Aug.	7.5	3.2	2.9	13.4	12.2
	13 Sept.	8	4.8	4.1	20.6	17.7
Sauer	12 May	6	0.0	—	0.1	—
	1 June	7	1.3	1.0	3.5	2.6
	22 June	8	6.0	4.1	15.3	10.3
	13 July	6	2.3	1.7	10.1	7.6
	4 Aug.	7.5	5.3	4.3	17.7	14.3
	23 Aug.	8	3.9	3.2	14.6	12.1
	14 Sept.	7.5	3.7	3.3	17.1	15.5

TABLE C. (*Concluded*)

	Date	Depth (m)	PP > 250 μm (mg/m^3)	ZP > 250 μm (mg/m^3)	% PP > 250 μm / TP	% ZP > 250 μm / TP
Twin	26 May	8	1.2	0.8	3.8	2.6
	14 June	9	3.0	2.3	18.4	14.0
	5 July	5	3.3	2.6	23.2	18.7
	26 July	5	1.8	1.3	12.8	9.2
	18 Aug.	5	2.6	1.8	19.5	13.4
	8 Sept.	6	2.4	2.0	21.8	18.5
Shallow lakes						
Baptiste N.	18 May	3	1.3	1.2	1.1	1.1
	8 June	6	1.6	1.0	3.2	2.1
	29 June	4	3.5	2.4	6.7	4.6
	20 July	4	9.8	9.0	15.0	13.7
	10 Aug.	3	5.0	3.9	7.4	5.8
	1 Sept.	4	7.6	7.0	7.9	7.2
	21 Sept.	4	13.0	13.6	13.4	14.0
Lessard	25 May	4	4.6	1.9	10.0	4.2
	9 June	4	6.4	3.4	18.3	9.7
	21 June	3	1.2	0.6	5.7	2.5
	3 Aug.	3.5	7.0	5.0	19.2	13.8
	24 Aug.	3	6.9	3.1	21.4	9.7
Mink	18 May	7	1.2	1.4	2.2	2.6
	31 May	6	3.9	3.4	10.9	9.6
	6 July	7	2.9	2.1	7.6	5.3
	27 July	5	3.4	2.4	9.6	6.8
	17 Aug.	3	4.5	3.3	5.5	4.0
	7 Sept.	3	9.0	6.1	12.8	8.7
Wizard	26 May	5	3.7	2.0	7.0	3.9
	14 June	6	3.8	2.1	9.6	5.4
	5 July	5	4.1	3.4	8.2	6.8
	26 July	3	1.1	0.6	2.0	1.2
	18 Aug.	3	0.8	0.5	1.5	0.8
	8 Sept.	2.5	0.9	0.5	1.4	0.8
	27 Sept.	3	1.0	0.7	1.7	1.2
Unclassified						
Hasse	11 May	7	0.0	—	0.0	—
	31 May	6	1.3	0.4	3.8	1.2
	15 June	7	3.3	1.7	10.2	5.3
	6 July	7	4.1	3.2	13.1	10.2
	27 July	6.5	5.4	3.9	23.9	17.1
	17 Aug.	6	2.9	2.3	12.7	9.9
	7 Sept.	7	2.7	2.3	13.3	11.1
	27 Sept.	4.5	2.7	2.2	11.1	9.1

Behavioral Response of Blacknose Dace (*Rhinichthys atratulus*) to Varying Densities of Predatory Creek Chub (*Semotilus atromaculatus*)

Douglas F. Fraser and Edward E. Emmons[1]

Department of Biology, Siena College, Loudonville, NY 12211, USA

Fraser, D. F., and E. E. Emmons. 1984. Behavioral response of juvenile blacknose dace (*Rhinichthys atratulus*) to varying densities of predatory creek chub (*Semotilus atromaculatus*). Can. J. Fish. Aquat. Sci. 41: 364–370.

We investigated the behavioral response of juvenile blacknose dace (*Rhinichthys atratulus*) to varying levels of predation risk by varying the density of predatory creek chub (*Semotilus atromaculatus*) and amount of structure in compartments of an artificial field stream. When structure in predator locations was low, dace did not avoid predators during the day but did at night, responding equally regardless of predator density. When structure was increased, the strength of avoidance at night was dependent on both the amount of structure and density of predators. Predators in experimental compartments caused dace to move to other locations of the stream. By moving away from predators, dace gain a short-term benefit in avoiding predation and a long-term benefit by reducing the chance of becoming trapped in pools with piscivorous fish when water levels in a natural stream drop. However, this shift could reduce feeding if dace move to locations poor for foraging or high in density of dace.

Nous avons étudié le comportement de jeunes naseux noirs (*Rhinichthys atratulus*) en réponse à divers niveaux de risque de prédation en faisant varier la densité de mulets à cornes (*Semotilus atromaculatus*) prédateurs et le numbre d'éléments dans les compartiments d'un cours d'eau artificiel sur le terrain. Quand la structure des compartiments est telle que le nombre d'endroits accessibles aux prédateurs est faible, les naseux n'évitent pas ces derniers le jour, mais les évitent la nuit, les réactions étant les mêmes, quelle que soit la densité des prédateurs. Avec une structure plus élaborée, l'intensité de la réaction d'évitement la nuit dépend à la fois de la structure et de la densité des prédateurs. Les prédateurs présents dans des compartiments expérimentaux forcent les naseux à se réfugier en d'autres endroits du cours d'eau. En s'éloignant des prédateurs, les naseux retirent un avantage à court terme par évitement de la prédation et un avantage à long terme par diminution du risque d'emprisonnement dans des fosses habitées par des poissons piscivores quand le niveau de l'eau baisse dans un cours d'eau naturel Cependant, ce déplacement pourrait causer une alimentation réduite si les naseux se réfugient dans des endroits peu propices à la recherche de la nourriture, ou si la densité des naseux est déjà élevée à ces endroits.

Received March 28, 1983
Accepted November 8, 1983

Reçu le 28 mars 1983
Accepté le 8 novembre 1983

Studies of the behavioral responses of prey to predators have usually treated predation risk as a discontinuous variable, i.e. high, low, present, or absent (see Stein 1979 for a review), even though in nature, risk probably varies continuously in response to predator density and environmental factors such as light (Emery 1973; Helfman 1982) and proximity of shelter (Stein and Magnuson 1976; Helfman 1981). The response of prey to levels of risk imposed by variations in predator density is especially important when predator and prey use the same patches (Krebs 1980). For example, risks should be greater for a young fish in a pool containing several predators as opposed to one with a single predator. This aspect of the response of prey to predators has received little attention (but see Potts 1981).

Small headwater streams are unique compared with larger streams in that pools, separated by riffles, tend to be discrete habitat patches where piscivorous fish and their prey are often found together (Fraser and Sise 1980). Recently, Fraser and Cerri (1982) showed that structured locations in an artificial field stream had higher carrying capacities for juvenile blacknose dace (*Rhinichthys atratulus*) and creek chub (*Semotilus atromaculatus*) than unstructured ones and that piscivorous adult chub caused the young fish to alter their use of the stream. However, they avoided unstructured locations with adults more than structured ones and avoided locations with adults less when light levels were high. Thus, structure and bright light lessened the intensity of avoidance. In those experiments the density of predators and amount of structure were fixed.

The purpose of our study was to test the response of dace to varying densities of chub and amount of structure. We predicted (1) risk should increase with the density of predators, at least at relatively low densities of predators, when interference between predators would be minimal, and dace should adjust their response to risk, (2) increasing structure in the habitat should lessen risk (Cooper and Crowder 1979; Crowder and Cooper 1982; Savino and Stein 1982) and, consequently, the avoidance response, at all densities of predators, and (3) daylight should

[1]Present address: Department of Biological Sciences, Bowling Green State University, Bowling Green, OH 43403, USA.

lessen risk (Helfman 1982; Hanych et al. 1983; Cerri 1983) because the reactive distance of the prey is greater in bright than dim light, so that avoidance at all densities of predators should be less in daylight than in twilight or darkness. Lastly, we asked if dace would clump in unstructured locations that lacked predators. We expected a clumped rather than a scattered distribution because unstructured locations varied slightly with respect to such features as flow rate and depth of bottom substrate.

Materials and Methods

Adult creek chub were electroshocked from pools in second-order headwater streams in Albany County, New York, where they are predators of blacknose dace (the stomachs of 11 of 24 adults collected in Albany county, 1975–79, contained one or more fish, of which six were dace, seven were digested and could not be identified, and two were other species). Dace were seined from headwater streams in Albany County, New York.

Experiments were conducted in two identical, artificial, wooden streams described in Fraser and Cerri (1982). Features essential to these experiments are (i) streams were located in the bed of a natural stream, (ii) each stream was 0.42 m wide × 14.4 m long, partitioned serially by dividers into 12 equal-sized compartments of 1.2 m each, which were screened (mesh size = 12.7 × 12.7 mm) so that the dace but not the chub could pass through (dace could swim unimpeded from compartment to compartment), and (iii) each compartment was fitted with a hinged drop gate such that when the water flow was stopped, the gates could be simultaneously dropped, isolating all 12 compartments.

To test our predictions, we selected as treatment compartments four compartments in both streams. Treatment compartments were used to manipulate predator density and structure. The extent to which dace avoided treatment compartments was assessed by counting the dace in treatment compartments both in the presence and absence of chub.

Sampling Procedure

We used three levels of predator density (one, two, and three per treatment compartment) and two levels of structure (one and two pipes per structured treatment compartment). Using the two streams, experiments were conducted sequentially beginning with the controls (see next section). We compared the number of dace present in treatment compartments of the two streams to ascertain if they were using the streams similarly. We found no significant differences (Mann–Whitney U test all $P > 0.05$). For each experiment we stocked about 48 juvenile dace (range = 30–50 mm total length (TL), $\bar{x} = 36.1$, 2 SE = 1.01), dipped from a holding pool containing several hundred. To sample fish we dropped the gates and made visual counts of the dace in all compartments. In each experiment we sampled twice daily for 6 d, once during daylight (10:30–16:00) and once in the dark (19:00–01:00). Night samples were taken with the aid of a 6-V headlamp. In preliminary experiments with free-ranging fish, we found predators to be most active at twilight, and both species were usually resting on the bottom, rarely shifting compartments, at night. Thus, we felt confident that the posttwilight locations of the dace reflected the results of the predator–prey interactions that occurred at twilight. To minimize disturbance during high activity, we confined our sampling to after evening twilight.

At the end of each 24 h we dipnetted the dace from the streams, returned them to the holding pool, mixed them, and then withdrew an equal number that were again restocked randomly throughout the streams. Thus, each day constituted an independent replicate, and each experiment was replicated six times.

The total counts of dace present in each stream fluctuated somewhat from day to day due to undetermined causes, e.g. predation, escapes, and fish missed in counting. Of fifty 24-h periods we recorded a loss of dace 19 times (range of numbers missing = 1–10, median = 3). We did not determine how many fish were lost to predators, but it was low and did not account for the differences in numbers of fish found in the experimental and control compartments. The small fluctuations did not affect the results because these were the same in the control and experimental replicates (Mann–Whitney U test, two-tailed, six comparisons, $N_1 = N_2 = 11$, all $P > 0.05$). We replaced lost fish at the end of each 24-h period, keeping the sample size close to the original.

Treatment Compartments

We selected 4 of the 12 compartments as treatment compartments in which we manipulated predator densities and structure. Empty compartments, i.e. nontreatment compartments, were on either side (up and downstream), and the fish always had a nearby retreat. Two of the treatment compartments were made structurally complex (structured treatment compartments) by adding a 7.5 × 20.0 cm pipe (we used pipes rather than logs or rocks because of the convenience in standardizing their size and ease of handling), whereas the two remaining treatment compartments were left empty (unstructured treatment compartments). In each stream the number of dace per treatment compartment was monitored for 6 d in the absence of predators (control). We also counted the dace in the eight nontreatment compartments, but these counts were for the purposes of adjusting stream totals at the end of the day and for determining if group size increased in locations without predators. They were not used in the analysis of prey response to predators in treatment compartments. At the end of 6 d we added a second pipe to the structured compartments and repeated the entire procedure.

Predator density was manipulated so that in any one experiment each of the four treatment compartments had the same density of predators, ranging from one to three. Chub (range = 100–150 mm TL, $\bar{x} = 130$, 2 SE = 4.0) were assigned to treatment compartments by means of a table of random numbers.

Data Analysis

We analyzed treatment effects in the following sequence: (1) amount of structure (one pipe vs two pipes), (2) presence or absence of structure (structure vs unstructured treatment compartments), and (3) time of day (day vs night). For each of these variables we compared number of dace found in treatment compartments (six replicates) at each chub density with the respective control using the Mann–Whitney U test (two-tailed). Since we made three comparisons using the same control, the probability of committing a type one statistical error on the third comparison, using $\alpha = 0.05$, is >0.05, whereas it is <0.05 if α is set at 0.01 (Sokal and Rohlf 1981). Thus, for these tests we set the rejection level at 0.01. To test for interactions among predator density, structure, and time of day we constructed

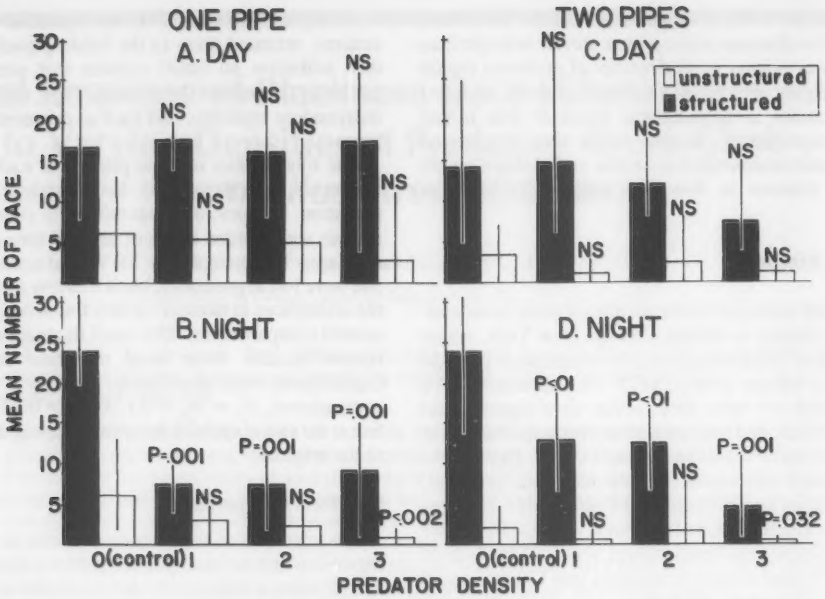


FIG. 1. Number (mean for six replicates) of dace in treatment compartments at different densities of creek chub in day and night when structured compartments contained one pipe and two pipes. Vertical lines = range. Probabilities are for the comparison of that predator density with the control shown at the left of each histogram (Mann–Whitney U test). NS = not significant.

three-way contingency tables (predator density × time of day × structure) and employed a multidimensional contingency table analysis (MDCTA). Since the test is less familiar than analysis of variance (ANOVA), we point out the characteristics that are important to understanding our usage of MDCTA. To test for the significance of an interaction, MDCTA generates an expected table based on a log-linear model (Bishop et al. 1975) that includes all interaction terms (analagous to the interaction terms of an ANOVA model) and an expected table based on a log-linear model from which the specific term of interest has been deleted. Each expected table is compared with the observed by the likelihood ratio statistic (Sokal and Rohlf 1981), which is distributed as chi-square. The likelihood ratio chi-square (G^2) is additive, so that the difference in the G values of the two models is a test of the effect of the term left out of the second model. The difference G value is also distributed as chi-square. It is this value that we give in the tabled results. The full analysis involved repeating the above procedure, stepwise, beginning with the highest order interaction (the three-way interaction), for each interaction term. Analysis of the three-way table required testing a large number of models, increasing the probability of making a type one error. Thus, we again set the rejection level at $\alpha = 0.01$. We used the University of California BMDP-79 biomedical computer program (Dixon and Brown 1979) to carry out MDCTA.

We tested the effect of predators on use of nontreatment compartments by tallying the number of times a dace was found alone, in groups of 2, 3,...,15+ in nontreatment compartments, where group size was the number of fish in the compartment. We compared the cumulative frequency of rank-ordered group sizes at each level of predator density when one and two pipes were present with that of the controls using the Kolmogorov–Smirnov two-sample test (K & S test). Because we predicted that group size in nontreatment compartments would increase when predators were present in treatment compartments, these tests were one-tailed. We used the test statistic (D) to calculate chi-square as $4D^2(n_1n_2/n_1 + n_2)$ with df = 2 and $\alpha = 0.05$ (Siegel 1956).

Results

Behavioral Observations

When structured treatment compartments contained a single pipe, dace did not avoid predators during the day (Fig. 1A) but did at night (Fig. 1B, $P < 0.001$). Whereas their response to structure at night was similar at all densities of predators, it was dissimilar in unstructured treatment compartments where they avoided three predators ($P < 0.002$) but not one or two ($P > 0.01$). The conspicuous difference in dace density (Fig. 1) for structured versus unstructured treatment compartments points out the strong effect of structure on the response of the dace. Dace response depended to a significant degree on the interactions of structure (presence or absence) and predator density (Table 1). A lack of significant interactions between time of day, predator and structure, and time indicated that each of these two variables were independent of one another in affecting the response of dace at each predator density. The three-way interaction was not significant.

When the structured treatment compartments contained two pipes, dace responded as they did with one; they did not avoid predators during the day (Fig. 1C) but did at night (Fig. 1D). As with one pipe, a conspicuous structure effect independent of density of the predator is shown in Fig. 1C and 1D; dace were always more abundant in structured than unstructured treatment compartments. We found important differences, however, in

TABLE 1. Results of MDCTA for the 2 × 2 × 3 table (structure × time of day × predator density) for the number of dace in treatment compartments, summed for six replicates. The G value is the likelihood ratio chi-square for the difference between a model containing all interaction terms and one that excludes only the specified interaction.

Interaction	G value	df	P
One pipe			
Time–predator	0.19	2	0.910
Structure–predator	12.87	2	0.002
Structure–time	0.01	1	0.929
Structure–time–predator	1.66	2	0.436
Two pipes			
Time–predator	3.40	2	0.182
Structure–predator	7.95	2	0.019
Structure–time	1.77	1	0.183
Structure–time–predator	0.06	2	0.971
One or two pipes			
Time–predator	0.74	2	0.689
Structure–predator	27.88	2	0.000
Structure–time	18.56	1	0.000
Structure–time–predator	2.76	2	0.252

the use of structured treatment compartments at night. When two pipes were present, dace avoided three predators more than they did one or two. They avoided one and two predators about equally. However, when only one pipe was present, avoidance was the same at all predator densities. Avoidance was not as strong at predator densities one and two when two pipes were present as with one pipe (compare Fig. 1B and 1D).

Notice that at night, dace avoided unstructured treatment compartments to the same extent, regardless of predator density, in both the one- and two-pipe experiments (compare Fig. 1B and 1D), except at the highest density (two pipes). Because unstructured treatment compartments were untouched when pipes were added to the structured ones, dace were using compartments of the artificial stream similarly in successive experiments.

The results of MDCTA revealed important differences between the one- and two-pipe experiments in that, with two pipes, none of the interactions were significant at $\alpha = 0.01$ (Table 1). The amount of structure appears important because the response to structure was always independent of predator density (compare the histograms for structure with those for no structure in each panel of Fig. 1). Therefore, we tested for the presence of an interaction between amount of structure (one vs two pipes) and predator density. We again constructed a 2 × 2 × 3 table, this time substituting amount of structure for the presence or absence of structure. The other two variables, time of day and predator density, remained as before. The results of MDCTA showed that both the amount of structure–predator density and the amount of structure–time of day interactions were significant ($P < 0.001$) but not the time of day–predator density or the three–way interactions (Table 1).

Dace in Nontreatment Compartments

The group sizes (group size = number of fish in a compartment) of dace present in nontreatment compartments increased significantly over controls only at night (Table 2), a result that was expected because during days, dace tended to be in structured treatment compartments. However, with one pipe in structured compartments, group size in nontreatment compartments increased significantly at predator densities one and two ($P < 0.05$), and at three predators the groups tended to be larger, although not significantly so ($P > 0.05$) (Table 2). When a second pipe was added, group sizes did not change significantly at predator densities one and two ($P > 0.05$) but did at density three ($P < 0.05$). Note that fish were not randomly distributed among nontreatment compartments, nor did they increase evenly when predators were added to treatment compartments. Numbers of dace increased in compartments adjacent (2, 4, 9, 11) to the structured ones (3, 10) when a single predator was present in treatment compartments (Fig. 2). The results in Fig. 2 reflect those obtained for the remaining predator densities in which there were significant increases in group size ($P < 0.01$, Mann–Whitney U test).

Discussion

Effect of Predator Density and Structure

We addressed the important issue of how prey fish in a patchy environment respond to variations in risk posed by different levels of predator density when certain desirable patches are also occupied by predators. Perhaps the most salient finding was that dace appeared to minimize risk. That is, in locations without structure that also contained predators, dace avoided a single predator as strongly as they did three. When structure in the patch increased, dace avoided predators less than they did in unstructured places. However, with one exception (the difference in response to densities two and three in the two-pipe experiment) they did not appear to respond to levels of risk posed by different densities of predators.

The lack of an association between the strength of the avoidance response and predator density, at least at the low amounts of structure and predator density, may mean that there were enough other locations with sufficient food that dace did not need to assess risk. However, dace did take risks by entering structured treatment compartments, at all predator densities, suggesting that this was not the case. Cerri and Fraser (1983) found that most dace had empty stomachs unless the experimental stream was supplemented with food. Thus, if our assumption that predator density and risk are correlated is correct, the fact that dace took risks but did not adjust their response to changes in predator density suggests that they did not discriminate levels of risk.

The strong affinity of the dace for shelter is not surprising, but it is of interest that dace responded differentially to the different amounts of structure. This point is underscored by the observation that when two pipes were present, dace avoided three predators significantly more than they did one or two. Structure and predator density depended on one another in affecting the response of the dace. Thus, in addition to predator density, amount of structure in the habitat needs to be considered when predicting foraging modes and habitat use patterns of young fish.

The response of the dace indicates an interaction between amount of structure and predator density. Although we assume that the pipes, like rocks or logs, afford cover, their precise role is not clear. For example, if chub were territorial, one to a pipe, a third individual would be left out and more visible to a dace

TABLE 2. Results of the K & S two-sample test for group size of dace in nontreatment compartments when predators were present compared with the controls without predators (N_1 = number of groups in experimental sample; N_2 = number of groups in control sample; $*P < 0.05$).

	Day			Night		
Predator density	N_1/N_2	D	Chi-square	N_1/N_2	D	Chi-square
One pipe						
1	44/36	0.116	1.066	43/39	0.311	7.912*
2	37/36	0.202	2.978	42/39	0.317	8.128*
3	39/41	0.130	1.351	43/35	0.242	4.519
Two pipes						
1	24/35	0.153	1.333	38/37	0.156	1.825
2	36/37	0.145	1.535	35/36	0.185	2.429
3	39/35	0.110	0.893	42/37	0.299	7.034*

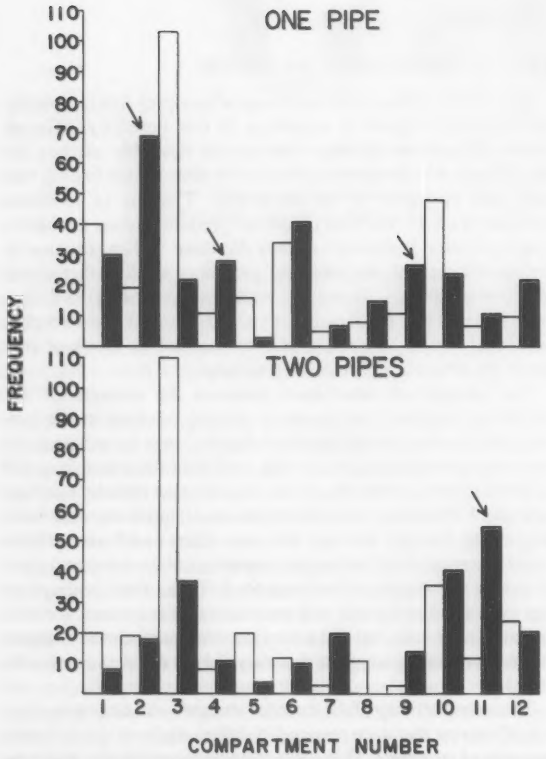


FIG. 2. Number of dace, summed for six replicates, at night, in all compartments of the artificial stream when a single predator was present in treatment compartments. Arrows direct attention to conspicuous increases over controls in compartments adjacent (2, 4, 6, 7, 9, 11) to structured ones (3, 10). Open bars = control; shaded bars = predators present.

entering the compartment, accounting for the jump in the degree of avoidance when predator density was increased from two to three. However, this seems unlikely because chub hide in the pipes during the day and are out at twilight and during the night (Cerri 1983; Fraser 1983). Further, these experiments used only nonbreeding adults, which appear not to be territorial (Ross 1977); we often observed more than one chub in a pipe.

Effect of Daylight

Time of day always significantly affected prey response to predators. Dace entered structured treatment compartments during the day to the same extent as they did in the control, regardless of predator density. Thus, bright light tends to reduce risk, as noted by others (Benzie 1965; Hall et al. 1979; Helfman 1982; Cerri 1983; Hanych et al. 1983), and may help explain why in daylight in natural streams one often observes young fish in the same pools as predatory adult chub.

Effect of Predators on Use of Unstructured Treatment Compartments

Given that the density of predators was the same in all treatment compartments during a single experiment, it seems anamolous that dace did not significantly avoid the unstructured treatment compartments at night, as they did the structured ones. Certainly these should have been higher risk places than those with structure. We noted that the numbers of dace in unstructured treatment compartments was always very low, often zero, even in the controls. Structured treatment compartments attracted many fish so that when predators were added it was possible to detect a significant reduction in dace.

Group Size in Nontreatment Compartments

One of the potential costs to young dace of shifting foraging patches is that the density of prey fish may increase in predator-free locations, lowering the profitability of those patches (e.g. Fretwell 1972). Here, during periods of high risk (predators present), group size in nontreatment compartments increased. Of course, if dace were avoiding compartments with predators, their numbers would have to increase elsewhere. The important point is that their numbers increased in some nontreatment compartments and not in others. The clumping indicated that some locations, especially those nearest structured treatment compartments, were preferred over others. We cannot rule out the possibility that the dace were schooling in response to predation risk. Regardless of the precise cause of the increase in group size, the consequences are the same: the

potential for increased intraspecific competition in predator-free locations.

Costs and Benefits of Avoiding

Given that young dace tended to avoid high-risk situations (pools with low structure) and treated all levels of risk similarly (one predator is as dangerous as three), we may ask about the costs and benefits of such behavior. An immediate benefit of always minimizing risk is, of course, the avoidance of predation, but other, longer term benefits may accrue. Headwater streams are notoriously subject to variations in water flow, and flow reductions during dry periods are common (Paloumpis 1956, 1958; Lotrich 1973; Tramer 1977), and at these times young fish may be trapped in pools with predators. Under these circumstances a single predator is likely to be as dangerous as several, especially if structure is sparse. On the other hand, avoidance of predators by shifting patch use may have associated costs, such as the reduction in foraging efficiency if shifts are to patches that are low in resources, crowded, or both. In headwater streams, pools that are good for foraging invertebrate prey, i.e. deep pools with slow-flowing water and leaf and debris accumulations (Egglishaw 1964; Mackay 1969; Mackay and Kalff 1969; Allan 1975), also attract large predatory fish (Saunders and Smith 1962; Fraser and Sise 1980). If predators and food cooccur in pools, reduced foraging efficiency may be a cost associated with shifting to predator-free locations, or of increased intraspecific competition when shifts are to already crowded patches (Sih 1980, 1982). Reduced foraging may jeopardize survival because fish often experience disproportionately high predation rates when small (e.g. Forney 1974; Nilsson 1979), and survival may depend on rapid growth through the vulnerable size range (Larkin and Smith 1954). Furthermore, patch shifts from pools with good cover may subject prey to increases in risk from avian or terrestrial predators (LeCren 1965).

Our results have implications for current interpretations of resource depression and optimal foraging theory. The response of the prey should have consequences for how predators should be spaced in the habitat (Brown and Orians 1970; Charnov, et al. 1976; Potts 1981). Had the prey responded as we predicted, by directly varying the strength of their avoidance response with predator density, one would predict that predators attempting to forage on young fish should avoid clumping, all else being equal. Our findings suggest that in pools with low structure it will make no difference to the predators whether they are clumped or not because dace will avoid all densities about equally. However, as the amount of structure increases, predator densities will make a difference in the avoidance response of the dace, so that increases in clumping by the predators will have increasingly negative effects on the number of dace present in the pool. Of course, as structure level increases, other factors will become important, such as the difficulty of catching dace in complex structure (Crowder and Cooper 1982; Savino and Stein 1982; Schlosser 1982). Our study addressed the question of prey response to varying predator densities. However, because optimal foraging theory needs to be able to predict the behavior of prey in predator-influenced systems, we will need to know more about the extent to which food levels and predator densities vary concordantly. If concordance is high, selection should favor prey that are able to weigh risks and benefits (e.g. food levels) and make foraging choices that are adaptive compromises (Sih 1980, 1982; Cerri and Fraser 1983).

Acknowledgments

We thank Karen Bosher, JoMarie Colucciello, Richard Cerri, James Duncan, Cheri Emmons, and Thomas Mottolese for help. We are grateful to Felicity Huntingford, Neil Ringler, Roy Stein, and Elizabeth Marschall for critiques of the manuscript and Neil Metcalfe for an insightful comment that improved the analysis. The experimental streams are located in the Albany Rural Cemetery, and we thank its director, Robert G. Killough, for his support. The study was supported by grant DEB-8116001 from the National Science Foundation.

References

ALLAN, J. D. 1975. The distributional ecology and diversity of benthic insects in Cement Creek, Colorado. Ecology 56: 1040–1053.

BENZIE, V. L. 1965. Some aspects of the antipredator responses of two species of stickleback. Ph.D. thesis, University of Oxford, Oxford, England. 149 p.

BISHOP, Y. M. M., S. E. FIENBERG, AND P. W. HOLLAND. 1975. Discrete multivariate analysis: theory and practice. MIT Press, Cambridge, MA.

BROWN, J. L., AND G. H. ORIANS. 1970. Spacing patterns in mobile animals. Annu. Rev. Ecol. Syst. 1: 239–262.

CERRI, R. D. 1983. The effect of light intensity on predator and prey behaviour in cyprinid fish. Anim. Behav. 31: 736–742.

CERRI, R. D., AND D. F. FRASER. 1983. Predation and risk in foraging minnows: balancing conflicting demands. Am. Nat. 121: 552–561.

CHARNOV, E. L., G. H. ORIANS, AND K. HYATT. 1976. Ecological implications of resource depression. Am. Nat. 110: 247–259.

COOPER, W. E., AND L. B. CROWDER. 1979. Patterns of predation in simple and complex environments, p. 257–267. *In* R. H. Stroud and H. Clepper [ed.] Predator–prey systems in fisheries management. Sport Fishing Institute, Washington, DC.

CROWDER, L. B., AND W. E. COOPER. 1982. Habitat structural complexity and the interaction between bluegills and their prey. Ecology 63: 1802–1813.

DIXON, W. J., AND M. B. BROWN [ED.] 1979. BMDP-79 biomedical computer programs P-series. University of California Press, Berkeley, CA. 880 p.

EGGLISHAW, H. J. 1964. The distributional relationship between the bottom fauna and plant detritis in streams. J. Anim. Ecol. 33: 463–476.

EMERY, A. R. 1973. Preliminary comparisons of day and night habits of freshwater fish in Ontario lakes. J. Fish. Res. Board Can. 30: 761–774.

FORNEY, J. L. 1974. Interactions between yellow perch abundance, walleye predation, and survival of alternate prey in Oneida Lake, New York. Trans. Am. Fish. Soc. 103: 15–24.

FRASER, D. F. 1983. An experimental investigation of refuging behaviour in a minnow. Can. J. Zool. 61: 666–672.

FRASER, D. F., AND R. D. CERRI. 1982. Experimental investigation of predator–prey relationships in a patchy environment: consequences for habitat use patterns in minnows. Ecology 63: 307–313.

FRASER, D. F., AND T. E. SISE. 1980. Observations on stream minnows in a patchy environment: a test of a theory of habitat distribution. Ecology 61: 790–797.

FRETWELL, S. D. 1972. Populations in a seasonal environment. Princeton University Press, Princeton, NJ. 217 p.

HALL, D. J., E. E. WERNER, J. F. GILLIAM, G. G. MITTLEBACH, D. HOWARD, C. G. DONER, J. A. DICKERMAN, AND A. J. STEWART. 1979. Diel foraging behavior and prey selection in the golden shiner (*Notomigonus crysoleucas*). J. Fish. Res. Board Can. 36: 1029–1039.

HANYCH, D. A., M. R. ROSS, R. E. MAGNIEN, AND A. L. SUGGARS. 1983. Nocturnal inshore movement of the mimic shiner (*Notropis volucellus*): a possible avoidance behavior. Can. J. Fish. Aquat. Sci. 40: 888–894.

HELFMAN, G. S. 1981. The advantage to fishes of hovering in shade. Copeia 1981: 392–400.

1982. Twilight activities and temporal structure in a freshwater fish community. Can. J. Fish. Aquat. Sci. 38: 1405–1420.

KREBS, J. R. 1980. Optimal foraging, predation risk and territory defence. Ardea 68: 83–90.

LARKIN, P. A., AND S. B. SMITH. 1954. Some aspects of introduction of the redside shiner (*Richardsonius balteatus*) on the Kamloops trout (*Salmo*

gairdneri kamloops) in Paul Lake, British Columbia. Trans. Am. Fish. Soc. 83: 161–175.

LECREN, E. D. 1965. Some factors regulating the size of populations of freshwater fish. Mitt. Int. Ver. Limnol. 13: 88–105.

LOTRICH, V. A. 1973. Growth, production, and community composition of fishes inhabiting first-, second-, and third-order streams in eastern Kentucky. Ecol. Monogr. 43: 377–397.

MACKAY, R. J. 1969. Aquatic insect communities in a stream on Mont St. Hilaire, Quebec. J. Fish. Res. Board Can. 26: 1157–1183.

MACKAY, R. J., AND J. KALFF. 1969. Seasonal variation in standing crop and species diversity of insect communities in a small Quebec stream. Ecology 50: 101–109.

NILSSON, N.-A. 1979. Food and habitat of the fish community of the region of Lake Vanern, Sweden. Inst. Freshw. Res. Rep. Drottningholm 0: 126–139.

PALOUMPIS, A. A. 1956. Stream havens save fish. Iowa Conserv. 15: 60.

1958. Responses of some minnows to flood and drought conditions in an intermittent stream. Iowa State Coll. J. Sci. 32: 547–561.

POTTS, G. W. 1981. Behavioural interactions between the Carangidae (Pisces) and their prey on the fore-reef slope of Aldabra, with notes on other predators. J. Zool. (Lond.) 195: 385–404.

ROSS, M. R. 1977. Aggression as a social mechanism in the creek chub (*Semotilus atromaculatus*). Copeia 1977: 393–397.

SAUNDERS, J. W., AND M. W. SMITH. 1962. Physical alteration of stream habitat to improve brook trout production. Trans. Am. Fish. Soc. 91: 185–188.

SAVINO, J. F., AND R. A. STEIN. 1982. Predator–prey interactions between largemouth bass (*Micropterus salmoides*) and bluegills (*Lepomis macrochirus*) as influenced by simulated, submerged vegetation. Trans. Am. Fish. Soc. 111: 255–266.

SCHLOSSER, I. J. 1982. Fish community structure and function along two habitat gradients in a headwater stream. Ecol. Monogr. 52: 395–414.

SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill Book Company, New York, NY. 312 p.

SIH, A. 1980. Optimal behavior: can foragers balance two conflicting demands? Science (Washington, DC) 210: 1041–1043.

1982. Foraging strategies and the avoidance of predation by an aquatic insect *Notonecta hoffmanni*. Ecology 63: 786–796.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. W. H. Freeman, San Francisco, CA. 859 p.

STEIN, R. A. 1979. Behavioral responses of prey to fish predators, p. 342–353. *In* R. H. Stroud and H. Clepper [ed.] Predator–prey systems in fisheries management. Sport Fishing Institute, Washington, DC.

STEIN, R. A., AND J. MAGNUSON. 1976. Behavioral response of crayfish to a fish predator. Ecology 57: 751–761.

TRAMER, E. J. 1977. Catastrophic mortality of stream fish trapped in shrinking pools. Am. Midl. Nat. 97: 469–478.

Characterization of Protease from the Myxosporean Salmon Parasite, *Henneguya salminicola*

E. Bilinski

Department of Fisheries and Oceans, Technology Services Branch, Technological Research Laboratory, Vancouver, B.C. V6T 1X2

N. P. Boyce[1]

Department of Fisheries and Oceans, Fisheries Research Branch, Pacific Biological Station, Nanaimo, B.C. V9R 5K6

and R. E. E. Jonas and M. D. Peters

Department of Fisheries and Oceans, Technology Services Branch, Technological Research Laboratory, Vancouver, B.C. V6T 1X2

Bilinski, E., N. P. Boyce, R. E. E. Jonas, and M. D. Peters. 1984. Characterization of protease from the myxosporean salmon parasite, *Henneguya salminicola*. Can. J. Fish. Aquat. Sci. 41: 371–376.

The biochemical properties of the protease(s) from the myxosporean parasite, *Henneguya salminicola*, occurring in the muscle of sockeye salmon, *Oncorhynchus nerka*, were examined. The cysts of the parasite contained a soluble, heat-labile protease, having maximal activity at pH 3.0 for hydrolysis of hemoglobin and 4.5 for hydrolysis of salmon muscle proteins. The inhibitions obtained from metal ions and from sulfhydryl group binding reagents suggest the involvement of sulfhydryl groups in the expression of enzyme activity. The enzyme required no preliminary activation by disulfide bond reducing agents and it had no obvious divalent metal ions requirement. The hydrolysis of salmon muscle by *H. salminicola* protease was strongly temperature dependent. Although proteolysis occurred at the highest rate at 30–40°C, the enzyme remained active in iced muscle. The proteolytic activity was arrested completely in frozen muscle but the enzyme was only slightly inactivated by a prolonged frozen storage (−28°C). The presence of the parasite had no marked effect on the texture of raw or cooked flesh.

Les propriétés biochimiques de la ou des protéases du parasite myxosporidien, *Henneguya salminicola*, se trouvant dans le muscle du saumon nerka, *Oncorhynchus nerka*, ont été examinées. Les kystes du parasite contiennent une protéase thermolabile soluble dont l'activité maximale se produit à un pH de 3,0 pour l'hydrolyse de l'hémoglobine et de 4,5 pour celle des protéines musculaires du saumon. Les inhibitions obtenues des ions métalliques et de réactifs fixateurs du groupe sulfhydril donnent à penser que les groupes sulfhydrils sont impliqués dans l'expression de l'activité enzymatique. L'enzyme ne requiert aucune activation préliminaire par des agents réducteurs des liens bisulfide et n'a aucun besoin apparent d'ions métalliques bivalent. L'hydrolyse du muscle de saumons par la protéase de *H. salminicola* dépend étroitement de la température. Bien que la protéolyse se produise à un taux maximal à 30–40°C, l'enzyme demeure actif dans le muscle placé dans la glace. L'activité protéolytique cesse complètement dans le muscle congelé, mais l'enzyme n'est que légèrement inactivé par l'entreposage à froid prolongé (−28°C). La présence du parasite n'a pas d'effet marqué sur la texture de la chair crue ou cuite.

Received August 22, 1983
Accepted November 23, 1983

Reçu le 22 août 1983
Accepté le 23 novembre 1983

The protozoan parasites occurring in the skeletal muscle of teleost fishes comprise several species of the class Myxosporea (Lom 1970). Although considered harmless to human consumers, they can reduce the commercial value of fish by affecting the texture or the appearance of the flesh. The spores of Myxosporea contain proteolytic enzymes that affect fish muscle. The proteases that occur in Myxosporea of the genus *Kudoa* have been partly studied in relation to the deterioration of the texture of the Pacific hake, *Merluccius productus* (Tsuyuki et al. 1982; Patashnik et al. 1982; Miller and Spinelli 1982), and of Kamchatka flounder, *Atheresthes evermanni* (Loseva 1976; Loseva and Kizevetter 1976). Various species of North American Pacific salmon are occasionally infected by the myxosporean *Henneguya salminicola* (Patashnik and Groninger 1964 and references cited therein; Boyd and Tomlinson 1965; Christensen and Ellemann 1976; Awakura and Kimura 1977; Margolis 1982). A recent study (N. P. Boyce, unpubl. data) has revealed infections in all five species of salmon resident in British Columbia, with infection prevalence as high as 79% in certain stocks and up to 533 cysts in an individual fish. There are indications that *H. salminicola* also exhibits proteolytic activity (Awakura and Kimura 1977), but little is known of the biochemical properties of the enzyme involved and of the factors controlling the postmortem proteolysis of salmon muscle.

A survey conducted by the Pacific Biological Station on the infection of various stocks of Pacific salmon by *H. salminicola* offered the opportunity to gather sufficient material to study the biochemical properties of the parasite's protease and to investi-

[1]Present address: Department of Fisheries and Oceans, Resource Research Branch, Ottawa, Ont. K1A 0E6.

gate the effects of temperature and other factors on the proteolysis of salmon muscle. The present report describes the results of this investigation conducted with sockeye salmon, *Oncorhynchus nerka*, infected with *H. salminicola*.

Materials and Methods

Sockeye salmon, *O. nerka*, from Henderson Lake, Vancouver Island, B.C., showing a high prevalence of *H. salminicola* infection, was used for this study. The fish were caught in mid-October during spawning migration using a trap located at the entrance to the lake. All fish were examined for the presence of macroscopic cysts in the muscle as part of the survey of *H. salminicola* distribution, and the identity of the parasite was confirmed by microscopic examination of the spores within the cysts. Heavily parasitized fish selected for the present study were stored frozen before use in enzyme preparations (1–4 mo, −28°C).

Determination of the Proteolytic Activity in Cyst Extracts

Cysts of *H. salminicola* (3–10 mm in diameter) were dissected from the partially thawed muscle. The heavily infected sockeye salmon yielded approximately 1–2 g of cysts per fish. The cysts isolated from 10–15 fish were pooled and homogenized with two volumes of ice-cold 0.5% KCl and the homogenate was centrifuged (10 000 × *g*, 30 min). The supernate solution was dialyzed against 0.5% KCl (24 h, 3°C) and centrifuged again to remove any precipitate. The resulting soluble enzyme solution showed no decrease in proteolytic activity during a 6-mo storage at −45°C. Hemoglobin (Worthington Biochemical Corp.) was used as a substrate for the assay of enzymic activity of cyst extracts. Unless otherwise stated, the incubation was conducted at 35°C for 60 min in citric acid–disodium hydrogen phosphate buffer (0.05 mol/L, pH 3.0) using 0.4 mL of 2% hemoglobin and 0.1 mL of enzyme solution in a total volume of 1 mL. With an appropriate enzyme concentration (5 μg protein N/mL) the hydrolysis of hemoglobin showed a linear increase during a 60-min incubation at 35°C. The reaction was stopped by adding 2.0 mL of 5% trichloroacetic acid. After centrifugation the products of protein hydrolysis were determined in the supernate according to the procedure of McDonald and Chen (1965), using a modification of Folin's reagent. The proteolytic activity was indicated by the increase in optical density at 700 nm over the preincubation values. All enzyme assays were conducted in triplicate.

In experiments on the effects of metal ions and other additives on proteolytic activity, the enzyme solution was preincubated for 30 min at 25°C in the presence of the additive before incubation according to the standard procedure described above. For the reversal of enzyme inhibition by cysteine, preincubation with the inhibitor (30 min, 25°C) was followed by a second preincubation (30 min, 25°C) in the presence of cysteine.

To determine the effect of pH on the proteolytic activity in cyst extracts the following buffers (0.05 mol/L) were used: pH 3.0–6.0 citric acid–disodium hydrogen phosphate, pH 6.0–8.0 disodium hydrogen phosphate–monosodium dihydrogen phosphate, and pH 9.0 boric acid–potassium chloride–sodium hydroxide. To obtain pH 1.0 and 2.0, citric acid–disodium hydrogen phosphate buffer was adjusted with HCl.

Determination of the Proteolysis of Salmon Muscle

To prepare homogenates of muscle infected with *H. salminicola*, the cysts were excised together with a portion of the adjacent flesh (approximately 1 cm^2). The material collected from several fish was pooled and thoroughly homogenized at ice temperature using an Omni-mixer. To prepare homogenates of noninfected muscle, the muscle was taken from the same group of infected fish in areas completely free of cysts. To control the proliferation of bacteria during incubation, 0.002% tetracycline was added to all homogenates. No other additives were used. The pH of the homogenized muscle ranged from 6.4 to 6.5.

For incubation at different temperatures and periods, 5-g aliquots of the undiluted homogenate were weighed into test tubes, which were stoppered and placed in a constant-temperature bath provided with a shaking device. To stop the reaction, 5 mL of 15% trichloroacetic acid was added after suspending the homogenate in 10 mL of water. The protein precipitate was separated by centrifugation (10 000 × *g*, 30 min) and the nonprotein nitrogen present in the supernate was determined by the Kjeldahl method (Steyermark 1951). The extent of proteolysis was indicated by the increase in nonprotein nitrogen over the value found before the incubation. All incubations were conducted in triplicate.

To determine the effect of pH on muscle proteolysis, 1-g aliquots of the homogenate were suspended in 9 mL of buffer solutions (0.1 mol/L) described in the previous section, and the proteolytic activity was measured using Folin's reagent according to the procedure used with cyst extracts.

In the experiment dealing with iced storage of eviscerated salmon the firmness of the muscle was measured after cooking using the Ottawa Texture Measuring System (Bilinski et al. 1977). In addition, the raw muscle was examined for changes in texture and general appearance.

Results

The general biochemical properties of *H. salminicola* protease(s) were determined using cyst extracts with hemoglobin as substrate. The tests on the effect of pH on the proteolytic activity (Fig. 1) indicated a narrow maximum near pH 3. There was no detectable activity above pH 7. The data in Table 1 show that

TABLE 1. Effect of metal ions on hydrolysis of hemoglobin by *H. salminicola* protease (cyst extracts).

Metal chloride (2.5 mmol/L)	Enzyme activity (% of control)[a]
Control (no additives)	100
$MgCl_2$	89.3±1.9
$CaCl_2$	97.7±2.1
$MnCl_2$	93.8±2.8
$FeCl_2$	50.2±1.9
$FeCl_3$	38.5±2.5
$CoCl_2$	78.7±7.4
$CuCl_2$	38.5±3.8
$ZnCl_2$	98.3±4.9
$CdCl_2$	99.6±6.8
$HgCl_2$	36.8±3.2

[a]Mean value ± SD (N = 3).

TABLE 2. Effects of various additives on hydrolysis of hemoglobin by *H. salminicola* protease (cyst extracts).

Additives	Concentration (mmol/L)	Enzyme activity (% of control)[a]
Control (no additives)		100
Sodium iodoacetate	1	24.2±0.5
Sodium iodoacetate	10	0
p-Chloromercuriphenyl sulfonate	1	37.6±2.9
Cysteine	1	147.6±2.3
Cysteine	5	149.6±1.9
EDTA	1	134.8±4.1
EDTA	10	118.7±5.9
EDTA	1	
+ cysteine	1	152.3±4.2
EDTA	1	
+ cysteine	5	153.7±1.9
1,10-Phenathroline	1	115.3±3.1
2,2′-Dipyridyl	1	98.3±2.0
Sodium-*p*-tosyl-lysine chloromethyl ketone	1	40.5±2.5

[a]Mean value ± SD ($N = 3$).

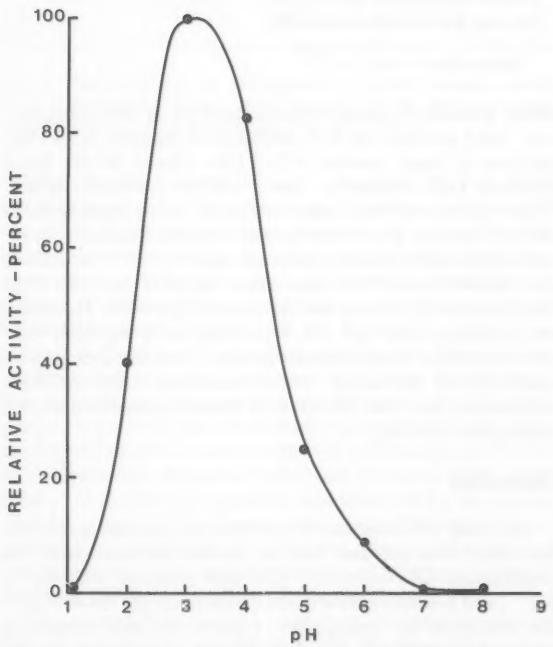


FIG. 1. Effect of pH on hydrolysis of hemoglobin by *H. salminicola* protease (cyst extracts).

Mg^{2+}, Ca^{2+}, Mn^{2+}, Zn^{2+}, and Cd^{2+} had little or no effect on proteolytic activity, while Fe^{2+}, Fe^{3+}, Cu^{2+}, Hg^{2+}, and Co^{2+} produced inhibition. Other additives affected enzyme activity (Table 2). Among compounds active upon the sulfhydryl groups, iodoacetate and *p*-chloromercuriphenyl sulfonate showed an inhibitory effect. On the other hand, cysteine, which is a known reducing agent of disulfide bonds, stimulated protease activity. Among reagents complexing metal ions, EDTA produced an increase in proteolytic activity. The stimulatory effects of cysteine and EDTA were not additive. Phenanthroline and dipyridyl had little or no effect. *p*-Tosyl-lysine chloromethyl ketone, a trypsin inhibitor, caused an inhibition of protease activity. The possible reversal by cysteine of the inhibition produced by metal ions and by sulfhydryl reagents was investigated in experiments reported in Table 3. In the presence of an excess of cysteine the inhibition brought about by Cu^{2+}, Hg^{2+}, and *p*-chloromercuriphenyl sulphonate was reversed completely, but iodoacetate caused an irreversible inactivation of the protease.

TABLE 3. Effect of cysteine on protease inhibitors in hydrolysis of hemoglobin by *H. salminicola* protease (cyst extracts).

Additives	Concentration (mmol/L)	Enzyme activity (% of control)[a]
Control (no additives)		100
$CuCl_2$	0.1	82.3±1.1
$CuCl_2$	0.1	
+ cysteine	1	139.8±1.03
$HgCl_2$	0.1	50.6±4.4
$HgCl_2$	0.1	
+ cysteine	1	160.0±1.1
p-Chloromercuriphenyl sulfonate	1	33.5±2.2
p-Chloromercuriphenyl sulfonate	1	
+ cysteine	2	130.6±2.1
Sodium iodoacetate	1	36.7±2.0
Sodium iodoacetate	1	
+ cysteine	2	43.3±1.6

[a]Mean value ± SD ($N = 3$).

The proteolysis of sockeye salmon muscle by *H. salminicola* was studied by comparing changes occurring in the infected and noninfected muscle. To ensure sufficiently uniform material for comparative tests, muscle homogenates, rather than intact muscle, were used in these experiments. At all temperatures

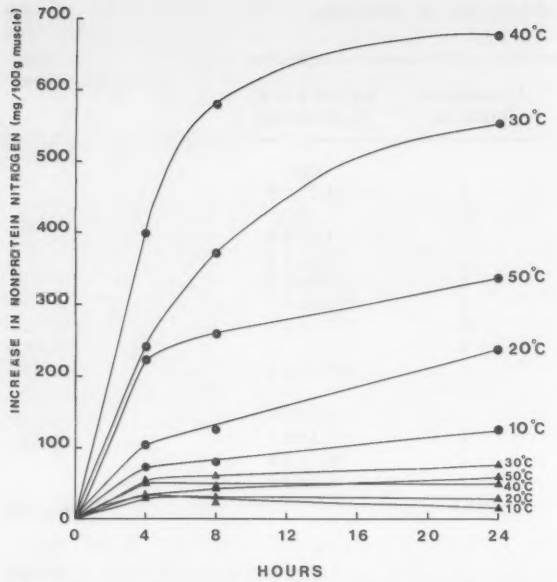


FIG. 2. Effect of temperature on proteolysis of sockeye salmon muscle (muscle homogenates). ▲, noninfected muscle; ●, muscle infected with *H. salminicola*.

TABLE 4. Proteolysis of sockeye salmon muscle during ice and frozen storage.

Storage conditions (muscle homogenates)	Nonprotein nitrogen (mg/100 g muscle)[a] Noninfected	Infected with *H. salminicola*
Storage in ice		
Starting material	446±6	506±2
3 d in ice	499±8	599±2
6 d in ice	490±5	677±6
Frozen storage		
Starting material	465±10	472±13
Starting material incubated for 4 h at 30°C	516±18	880±21
Increase due to incubation at 30°C	51	408
3 mo at −28°C	446±13	468±23
3 mo at −28°C followed by incubation for 4 h at 30°C	500±19	851±3
Increase due to incubation at 30°C	54	383
9 mo at −28°C	425±18	482±14
9 mo at −28°C followed by incubation for 4 h at 30°C	479±20	819±29
Increase due to incubation at 30°C	54	337

[a]Mean value ± SD (N = 3).

tested the proteolysis was much more pronounced in the presence of *H. salminicola* than in the noninfected muscle (Fig. 2). The *H. salminicola* protease showed the highest activity at 30–40°C, and at 50°C it was partially inactivated. At 20 and 10°C the proteolytic activity amounted to approximately 30 and 15%, respectively, of the maximum level. In additional tests, preincubation of the muscle homogenate at 85°C for 10 min caused a 75% decrease in proteolytic activity. In muscle homogenates of sockeye salmon stored in ice for up to 6 d the nonprotein nitrogen increased progressively in the infected muscle but showed little or no change in the noninfected muscle (Table 4). During a 9-mo storage at −28°C the proteolysis was arrested both in the infected and noninfected muscle. The stability of *H. salminicola* protease at −28°C was determined by measuring the enzyme activity before and after different periods of frozen storage (see values for 4-h incubations at 30°C in Table 4). After 9 mo of frozen storage the activity of the parasite protease decreased by less than 20%. The hydrolysis of salmon muscle by *H. salminicola* protease occurred at the highest rate at pH 4.5 (Fig. 3). At pH 6.5, closely approaching the normal pH of salmon muscle, the proteolytic activity amounted to less than 40% of the maximum level. Above pH 7.0, *H. salminicola* protease showed little or no activity. In noninfected muscle the proteolysis was most pronounced at pH 4.0–4.5.

In further experiments, not included in tables or figures, we found that a 3- to 16-d iced storage of the eviscerated sockeye salmon infected with *H. salminicola* resulted in no abnormal texture of the raw flesh or decrease in the firmness of the cooked flesh. In cooked samples the average shear press force values (kilograms) amounted to 49.0 ± 3.6 (12) for the noninfected flesh and 49.7 ± 1.1 (12) for the infected flesh. During iced storage of eviscerated salmon there were no noticeable changes in the appearance of the flesh in areas surrounding the cysts. The addition of up to 10% NaCl to muscle homogenates did not inhibit proteolysis caused by the parasite but at 20% concentration, NaCl produced an 80% inhibition of the proteolysis. The addition of liquid smoke (0.5–5.0%, Charso FP-10, Food Products Ltd., Montreal, Que.) had no inhibitory effect. Observations were also made on changes in the appearance of chinook salmon, *Oncorhynchus tshawytscha*, infected with *H. salminicola* during brining and cold smoking (25°C) according to a standard commercial procedure. Some of the cysts were disrupted during brining and water soaking of fish. However, the remaining cysts and cyst walls adherent to the flesh were very prominent in the smoked product, possibly reducing its suitability for marketing. Under conditions tested the flesh surrounding the cysts preserved a normal appearance during brining and smoking.

Discussion

Our study indicates that *H. salminicola* produces a soluble, heat-labile acid protease with no obvious divalent metal ion requirement. The reversible inhibition obtained with Cu^{2+}, Hg^{2+}, and *p*-chloromercuriphenyl sulfonate, and the irreversible inhibition by iodoacetate, suggest the involvement of sulfhydryl groups in the development of enzyme activity (Hochster and Quastel 1963). In this respect the *H. salminicola* enzyme differs from digestive proteases such as trypsin or pepsin (Walsh 1975). Although *H. salminicola* protease bears similarity to other sulfhydryl proteases, it has some distinctive characteristics. Plant proteases, such as papain, are inactive unless the disulfide bonds are reduced to free sulfhydryl groups by cysteine or other reducing agents (Smith and Kimmel 1960). For *H. salminicola* protease such preliminary activation was not obligatory although maximum activity was achieved in the presence of cysteine. It appears that some of the essential sulfhydryl groups of *H. salminicola* protease are already present in the native form of the enzyme. In addition to reduction of

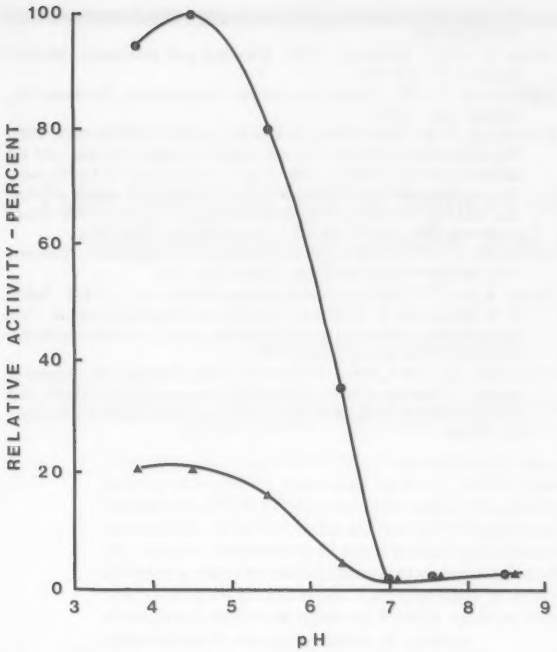


FIG. 3. Effect of pH on proteolysis of sockeye salmon muscle (muscle homogenates). ▲, noninfected muscle; ●, muscle infected with *H. salminicola*. Incubation at 35°C for 120 min.

disulfide bonds, removal of metal ions by EDTA or other chelators is necessary for full activity of papain. Such is not the case for *H. salminicola*. With regard to the lack of requirement for preliminary activation, *H. salminicola* protease resembles some bacterial proteases, e.g. the protease from *Proteus vulgaris* (Mills and Wilkins 1958). However, the optimum pH for the *P. vulgaris* protease is 9–10, whereas *H. salminicola* protease is the most active in the acid pH range. The observed inhibition of *H. salminicola* protease by different divalent metal ions cannot be ascribed entirely to reactivity with the sulfhydryl groups. A generally similar inhibition pattern, involving, e.g., inactivation by iron but not by zinc, was previously reported for certain microbial proteases (Sodek and Hofmann 1970). Like papain, *H. salminicola* protease was inhibited by the trypsin inhibitor *p*-tosyl-lysine chloromethyl ketone. This inhibition is attributed to inactivation of sulfhydryl groups rather than to specific binding of histidine active sites taking place in trypsin inhibition (Whitaker and Perez-Villasenor 1968).

The parasitic Protozoa are known to produce various types of proteolytic enzymes (von Brand 1979). The knowledge of the biochemical properties of proteases formed by the myxosporean parasites of fish is still fragmentary. The proteases from the genus *Kudoa*, occurring in different species of bottom fish, are similar to *H. salminicola* protease in being inhibited by compounds reacting with the sulfhydryl groups (Miller and Spinelli 1982) and in being active in the acid pH range (Patashnik and Groninger 1964; Loseva 1976; Tsuyuki et al. 1982). The acid protease from *K. thyrsitis*, found in the Pacific hake shows optimum activity at 35–40°C, which is similar to the protease from *H. salminicola*. *Kudoa paniformis*, occurring in some populations of the Pacific hake (Kabata and Whitaker 1981), contains a neutral protease with an activity optimum at 55–60°C (Tsuyuki et al. 1982). Loseva and Kizevetter (1976) reported that tryptophan and tyrosine are formed under the action of *Kudoa* spp. enzymes during the proteolysis of muscle of the Kamchatka flounder.

We suggest that the storage temperature is of major importance for controlling proteolytic degradation of salmon muscle by *H. salminicola*. The muscle proteolysis was the most pronounced at 30–40°C. Lowering the temperature to 20°C and below decreased to a large extent the proteolysis, but the parasite protease still remained active in iced muscle. Although proteolytic changes were arrested completely by freezing, the parasite protease was only slightly inactivated by a prolonged frozen storage. It would appear that under usual handling and processing conditions the infection by *H. salminicola* causes no softening of raw or cooked salmon flesh. In this respect *H. salminicola* differs from Myxosporea of the genus *Kudoa*. In Pacific hake (Patashnik et al. 1982; Tsuyuki et al. 1982) or Kamchatka flounder (Loseva and Kizevetter 1976) infected with *Kudoa* spp. the postmortem proteolysis leads to the development of a mushy texture, especially following cooking. This might be related to the fact that the spores of the genus *Kudoa* occur within the muscle fibres without encapsulation by connective tissue, whereas *H. salminicola* forms large intramuscular cysts with comparatively thick walls, which disintegrate slowly postmortem. It has been reported previously that the infection of salmon with *H. salminicola* leads, occasionally, to the appearance of isolated milky areas in the flesh (Patashnik and Groninger 1964; Boyd and Tomlinson 1965; Awakura and Kimura 1977). In our study the flesh itself did not become milky during ice storage or brining and cold smoking of infected salmon but it was noted that the release of white fluid from accidentally disrupted large cysts produced a milky appearance of the surface of the flesh.

Acknowledgments

We thank Dr L. Margolis, Pacific Biological Station, Nanaimo, B.C., for his critical review of the manuscript and Mr J. W. Boyd of the Vancouver Laboratory for performing some of the microscopic examinations.

References

AWAKURA, T., AND T. KIMURA. 1977. On the milky condition in smoked coho salmon (*Oncorhynchus kisutch*) caused by myxosporidian parasite. Fish. Pathol. 12: 179–184. (In Japanese, Fish. Mar. Serv. Transl. Ser. No. 4269, 1978)

BILINSKI, E., Y. C. LAU, AND R. E. E. JONAS. 1977. Objective measurement and control of the firmness of canned herring. Fish. Mar. Serv. Tech. Rep. No. 727: 22 p.

BOYD, J. W., AND N. TOMLINSON. 1965. Myxosporidian parasite from salmon. J. Fish. Res. Board Can. 22: 849–850.

CHRISTENSEN, N. O., AND G. ELLEMANN. 1976. Henneguya cysts in imported Pacific salmon. Saert. Dan. Vet. 59: 1057–1061.

HOCHSTER, R. M., AND J. M. QUASTEL. 1963. Metabolic inhibitors. Vol. 2. Academic Press, New York, NY. 753 p.

KABATA, Z., AND D. WHITAKER. 1981. Two species of *Kudoa* (Myxosporea: Multivalvulida) parasitic in the flesh of *Merluccius productus* (Ayres, 1855) (Pisces: Teleostei) in the Canadian Pacific. Can. J. Zool. 59: 2085–2091.

LOM, J. 1970. Protozoa causing diseases in marine fishes. *In* S. F. Snieszko [ed.] A symposium on diseases of fishes and shellfishes. Am. Fish. Soc. Spec. Publ. 5. Washington, DC. 526 p.

LOSEVA, A. V. 1976. Influence of Myxosporidia on the biochemical properties of the flesh of Kamchatka flounder. Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr. 99: 3–7. (In Russian)

LOSEVA, A. V., AND I. V. KIZEVETTER. 1976. Influence of Myxosporidia on

the technological properties of the flesh of Kamchatka flounder. Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr. 99: 8–10. (In Russian)

MARGOLIS, L. 1982. Parasitology of Pacific salmon — an overview, p. 135–226. *In* E. Meerovitch [ed.] Aspects of parasitology — a Festschrift dedicated to the fiftieth anniversary of the Institute of Parasitology of McGill University, 1932–1982. McGill University, Montreal, Que.

MCDONALD, C. E., AND L. L. CHEN. 1965. The Lowry modification of the Folin reagent for determination of proteinase activity. Anal. Biochem. 10: 175–177.

MILLER, R., AND J. SPINELLI. 1982. The effect of protease inhibitors on proteolysis in parasitized Pacific whiting, *Merluccius productus*, muscle. Fish. Bull. 80: 281–286.

MILLS, G. L., AND J. M. WILKINS. 1958. The isolation and properties of a protease from *Proteus vulgaris*. Biochim. Biophys. Acta 30: 63–70.

PATASHNIK, M., AND H. S. GRONINGER JR. 1964. Observations on the milky condition in some Pacific coast fishes. J. Fish. Res. Board Can. 21: 335–346.

PATASHNIK, M., H. S. GRONINGER JR., M. BARNETT, G. KUDO, AND B. KOURY. 1982. Pacific whiting, *Merluccius productus*: I. Abnormal muscle texture caused by Myxosporidian-induced proteolysis. Mar. Fish. Rev. 44(5): 1–12.

SMITH, E. L., AND J. R. KIMMEL. 1960. Papain, p. 133–173. *In* P. D. Boyer, H. Lardy, and K. Myrback [ed.] The enzymes. Vol. 4. Academic Press, New York, NY.

SODEK, J., AND T. HOFMANN. 1970. Microbial acid proteinases. Methods Enzymol. 19: 372–397.

STEYERMARK, A. 1951. Quantitative organic microanalysis. Blackston Co., Toronto, Ont. 134 p.

TSUYUKI, H., S. N. WILLISCROFT, Z. KABATA, AND D. J. WHITAKER. 1982. The relationship between acid and neutral protease activities and the incidence of soft cooked texture in the muscle tissue of Pacific hake, *Merluccius productus*, infected with *Kudoa paniformis* and/or *K. thyrsitis*, and held for varying times under different pre-freeze chilled storage conditions. Fish. Aquat. Sci. Can. Tech. Rep. No. 1130: 39 p.

VON BRAND, T. 1979. Biochemistry and physiology of endoparasites. Elsevier/North-Holland Biomedical Press, Amsterdam. 52 p.

WALSH, K. A. 1975. Unifying concepts among proteases, p. 1–11. *In* E. Reich, D. B. Rifkin, and E. Shaw [ed.] Proteases and biological control. Cold Spring Harbor conferences on cell respiration. Vol. 2. Cold Spring Harbor Laboratory, Cold Spring Harbor, NY.

WHITAKER, J. R., AND J. PEREZ-VILLASENOR. 1968. Chemical modification of papain. 1. Reaction with the chloromethyl ketones of phenylalanine and lysine and with phenylmethylsulfonyl fluoride. Arch. Biochem. Biophys. 124: 70–78.

NOTES

Fyke Net Catches as Indices of the Abundance of Brook Trout, *Salvelinus fontinalis*, and Atlantic Salmon, *Salmo salar*

P. M. Ryan

Fisheries Research Branch, Department of Fisheries and Oceans, P.O. Box 5667, St. John's, Nfld. A1C 5X1

Ryan, P. M. 1984. Fyke net catches as indices of the abundance of brook trout, *Salvelinus fontinalis*, and Atlantic salmon, *Salmo salar*. Can. J. Fish. Aquat. Sci. 41: 377–380.

The catch per unit effort (CPUE) data of brook trout (*Salvelinus fontinalis*) and Atlantic salmon (*Salmo salar*) in fyke nets set in two small lakes in central Newfoundland were compared with population densities estimated with Schnabel multiple mark–recapture experiments each spring and fall from 1978 to 1982. The catchability of brook trout did not differ significantly between lakes or seasons, and CPUE was an index of the relative abundance of trout within and between lakes. In contrast, the catchability of Atlantic salmon differed greatly between lakes and varied seasonally, being greater in the spring but less in the fall than the catchability of brook trout. Comparisons of relative salmon abundance between lakes or of the relative abundance of brook trout to Atlantic salmon within or between lakes require a correction for seasonal differences in the catchability of salmon.

L'auteur compare, d'une part, les données sur les prises par unité d'effort (PUE) dans le cas des ombles de fontaine (*Salvelinus fontinalis*) et des saumons de l'Atlantique (*Salmo salar*) pêchés à l'aide de verveux mouillés dans deux petits lacs de la partie centrale de Terre-Neuve et, d'autre part, les densités des populations évaluées à partir des données recueillies au cours d'expériences multiples de marquage et recapture de type Schnabel, expérience réalisées au printemps et à l'automne de 1978 à 1982. La capturabilité de l'omble de fontaine n'a pas varié de façon significative d'un lac à l'autre ni d'une saison à l'autre; en outre, les PUE ont constitué un indice de l'abondance relative de l'espèce dans chaque lac ou entre les lacs. Au contraire, le potentiel de capture du saumon de l'Atlantique a considérablement varié entre les lacs et d'une saison à l'autre: il était plus élevé que celui de l'omble de fontaine au printemps mais inférieur à celui-ci à l'automne. Il est nécessaire d'effectuer une correction pour les différences saisonnières de la capturabilité du saumon afin de comparer son abondance relative d'un lac à l'autre ou par rapport à l'abondance de l'omble de fontaine dans un lac donné ou entre les lacs.

Received June 23, 1983
Accepted October 11, 1983

Reçu le 23 juin 1983
Accepté le 11 octobre 1983

Information on the vulnerability of brook trout, *Salvelinus fontinalis*, and Atlantic salmon, *Salmo salar*, to fyke nets is of use to workers wishing to estimate the abundance of these fishes in lakes without harming large numbers of fish or conducting lengthy population estimates. Fyke nets are commonly used by fisheries personnel in the abundant small lakes of Newfoundland and elsewhere, and their use has recently been reviewed by Craig (1980). Catchability, the portion of a fish stock captured by a defined unit of effort, generally varies with such factors as species, season, net location, and fish size. However, no published reports have quantified the susceptibility of these salmonids to capture by fyke nets in lakes.

As a part of ongoing studies of small, central Newfoundland lakes, salmonid populations were censused by means of multiple mark–recapture experiments with fyke nets each spring and fall. During these studies, the catch per unit effort (CPUE) with fyke nets was strongly related to the densities of brook trout and Atlantic salmon, as estimated by the mark–recapture experiments. These relationships may be of use to other investigators in circumstances where fish kills are unacceptable or time is limiting.

Study Area

Headwater Pond (48°16′15″N, 55°29′39″W) and Spruce Pond (48°19′40″N, 55°28′24″W) are soft waters (mean conductance 33 $\mu S \cdot cm^{-1}$) typical of Newfoundland's many small brown-water lakes. They lie in a black spruce forest at the headwaters of the Northwest Gander River within the Department of Fisheries and Oceans' Experimental Ponds Area (Ryan 1982). Headwater Pond (area 76.1 ha, max. depth 3.3 m, mean depth 1.1 m) has one inlet and an outlet draining 3.5 km north to Spruce Pond (area 36.5 ha, max. depth 2.1 m, mean depth 1.0 m). Spruce Pond has an additional minor inlet and an outlet draining to the Atlantic Ocean. In addition to brook trout and Atlantic salmon, the lakes are populated by American eels (*Anguilla rostrata*) and threespine sticklebacks (*Gasterosteus aculeatus*). The Atlantic salmon are part of a sea-run stock, and those considered in the present study are the immature and

TABLE 1. Fishing efforts, catches, and population sizes (with 95% confidence intervals) of salmonids at the end of Schnabel population estimates in Headwater Pond.

Dates of Estimate	No. of net-nights	Brook trout		Atlantic salmon	
		No. captured	No. in population	No. captured	No. in population
May 18–30, 1979	88	609	1549 (1257–2018)	1941	2065 (1890–2273)
Sept. 12–Oct. 2, 1979	159	1977	2556 (2344–2810)	431	622 (518–779)
May 18–June 6, 1980	87	896	2252 (1897–2777)	1270	1520 (1367–1713)
Sept. 10–24, 1980	120	2151	3316 (3021–3674)	294	563 (436–793)
May 14–27, 1981	112	1117	1703 (1502–1966)	760	668 (592–766)
Sept. 16–Oct. 1, 1981	127	2843	4761 (4372–5226)	130	382 (249–819)
May 19–June 2, 1982	128	1398	3070 (2692–3571)	793	965 (845–1125)
Sept. 15–Oct. 5, 1982	168	1750	3645 (3252–4146)	130	551 (345–1361)
Average spring 1979–82	104	1005	2144	1191	1305
Average fall 1979–82	144	2180	3570	246	530

precociously mature forms. The lakes are usually ice-covered from December to April, and mean weekly mid-day water temperatures during the mark–recapture experiments ranged from 5 to 15°C in the spring and from 7 to 14°C in the fall.

Materials and Methods

Salmon and trout populations were censused concurrently each spring and fall by Schnabel's multiple mark–recapture method (Ricker 1975) commencing in 1978 in Spruce Pond and 1979 in Headwater Pond. Fish were captured in fyke nets, marked with adipose fin clips, pelvic fin clips, or caudal fin holes, and released throughout the lakes away from their location of capture. Each census was continued at least until recaptured fish were roughly 30–50% of the total catch over several days or, on occasion, catches remained consistently low.

Fyke nets were constructed of knitted nylon and had 5.5-m-long bodies with three throats in five 76-cm^2 aluminum frames, an outside iron frame opening of 1.2 m^2, two 7.6-m wings, and a 30.5-m leader. Stretched mesh size was 19 mm or, in one net in each pond in 1979 and 1980, 13 mm. Five nets in Spruce Pond and eight nets in Headwater Pond were fished at the same location during each census except that an additional net was used in Spruce Pond in the spring of 1978. Nets were set perpendicular from shore with the outside opening close to or breaking the water surface. Typically, the nets were hauled each day. Occasionally, nets were fished for 2–3 d or collapsed for similar periods.

The standard unit of fishing effort selected was a net-night or a single fyke net fished for a 24-h period. Catch was calculated as the cumulative total of all fish captured during each population estimate including fish killed and recaptured fish. CPUE was then the average number of fish captured in a single fyke net fished for 24 h. The relationship of CPUE to population density was examined by least-squares regression, and regression lines were compared by analysis of covariance (Dixon and Massey 1969).

Results and Discussion

Both brook trout and Atlantic salmon population sizes exhibited considerable seasonal and yearly variation (Tables 1 and 2). Trout in Headwater Pond increased in number over the summer months, decreased during winter, and showed an overall increase over the course of the study. The number of trout in Spruce Pond tended to decrease over the summer, increase during winter, and showed an overall increase over the study period. Such fluctuations in population sizes are not atypical of brook trout, as movements are influenced by such factors as water levels, temperatures, and population pressures (Scott and Crossman 1964; Power 1980). Salmon numbers in both lakes tended to decrease during the summer after the smolt run, increase in winter, and showed an overall decrease during the study. These fluctuations are indicative of the common use of lakes as overwintering and rearing areas by Atlantic salmon prior to smoltification in Newfoundland (Chadwick 1982).

Trout captured during the population estimates ranged in fork length from 56 to 368 mm and salmon were 50–323 mm. Population sizes were probably slightly underestimated due to a lesser movement and resultant lesser susceptibility to capture of the smallest fish. However, trout and salmon of 5–10 cm were relatively abundant in the fyke net catches of some years and rare in others. Similarly, the smallest of the two fyke net mesh sizes did not capture smaller fish than did the large mesh, indicating that the smallest fish were rarely caught in the lakes because most were still occupying stream habitats.

TABLE 2. Fishing efforts, catches, and population sizes (with 95% confidence intervals) of salmonids at the end of Schnabel population estimates in Spruce Pond.

Dates of Estimate	No. of net-nights	Brook trout		Atlantic salmon	
		No. captured	No. in population	No. captured	No. in population
May 18–26, 1978	54	615	988 (824–1234)	1641	2871 (2557–3273)
Sept. 14–Oct. 6, 1978	85	444	574 (418–712)	628	1198 (1006–1480)
May 18–25, 1979	40	669	1094 (917–1355)	2203	2755 (2516–3044)
Sept. 12–28, 1979	85	453	740 (610–939)	582	1328 (1091–1695)
May 19–June 6, 1980	50	500	1378 (1088–1878)	1857	1943 (1782–2135)
Sept. 10–24, 1980	75	849	1100 (959–1290)	571	1592 (1279–2107)
May 16–27, 1981	60	907	1206 (1053–1411)	1273	1725 (1537–1965)
Sept. 16–Oct. 1, 1981	80	1464	2083 (1863–2362)	812	1949 (1626–2432)
May 18–June 1, 1982	75	1547	1680 (1531–1861)	2113	2112 (1955–2297)
Sept. 15–Oct. 5, 1982	105	1390	1368 (1243–1522)	568	874 (736–1087)
Average spring 1978–82	56	848	1269	1817	2281
Average fall 1978–82	86	920	1173	632	1388

A greater fishing effort was applied in Headwater Pond, but because of its larger size, average fishing intensity was less (1.63 net-nights·ha^{-1} in Headwater Pond vs 1.95 net-nights·ha^{-1} in Spruce Pond). Spring population estimates required lesser fishing effort than the fall estimates in both lakes. CPUE data indicated that this was largely due to seasonal differences in salmon activity.

Brook trout CPUE was strongly related to trout population density in both Headwater ($r = 0.82$, $P < 0.05$) and Spruce ($r = 0.81$, $P < 0.01$) ponds. The regression of CPUE on density in Headwater Pond ($Y = 1.61 + 0.29X$) did not differ significantly from that in Spruce Pond ($Y = 1.18 + 0.35X$) in slope ($P = 0.68$) or intercept ($P = 0.37$). The two could be combined (Fig. 1) to yield a single relationship ($P < 0.01$) whose intercept was not significantly different from zero ($P = 0.43$). Thus, the CPUE of brook trout was an index of large differences in relative trout abundance both within and between lakes.

There was no evidence to indicate that trout catchability varied with season, although fall catch data provided the most precise estimates of relative abundance. The regression of CPUE on density based on fall data ($Y = 0.11 + 0.33X$) did not differ from the overall relationship in slope ($P = 0.80$) or intercept ($P = 0.49$), although the trend was stronger ($r = 0.90$, $P < 0.01$). The regression with the spring data was not statistically significant ($r = 0.64$, $P > 0.05$) and did not differ from the fall relationship in slope ($P = 0.95$) or intercept ($P = 0.26$).

Atlantic salmon CPUE was an indicator of relative salmon abundance within each of Headwater ($r = 0.98$, $P < 0.01$) and Spruce ($r = 0.81$, $P < 0.01$) ponds. The trend line in Headwater Pond ($Y = -4.59 + 0.97X$) had an intercept significantly different from zero ($P = 0.01$), while that in Spruce Pond ($Y = -17.78 + 0.77X$), because of a greater variance in data about the line, did not ($P = 0.13$). The two slopes did not differ significantly ($P = 0.64$), but the intercepts did ($P = 0.02$),

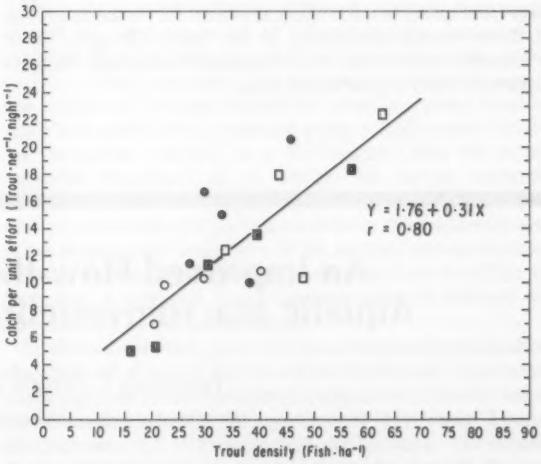


FIG. 1. Brook trout catches related to population densities in Spruce (solid symbols) and Headwater (open symbols) ponds. Circles and squares indicate spring and fall data, respectively.

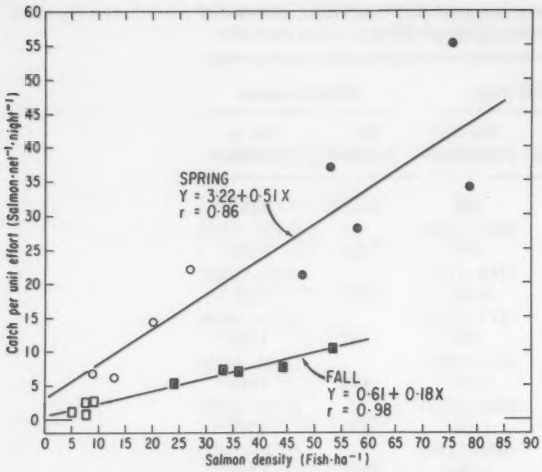


FIG. 2. Atlantic salmon catches related to population densities in Spruce (solid symbols) and Headwater (open symbols) ponds. Circles and squares indicate spring and fall data, respectively.

precluding the application of CPUE as a simple index of relative between-pond salmon abundance. The apparent differences in salmon catchability between ponds could be corrected for by compensating for season of capture. Separation of the data by season (Fig. 2) provided two significant relationships ($P < 0.01$) differing significantly in slope ($P = 0.04$), with intercepts not differing significantly from zero (spring, $P = 0.58$; fall, $P = 0.20$). Thus, if season of capture was taken into account, salmon CPUE was an index of marked differences in relative salmon abundance between the study lakes.

The marked decrease in the catchability of salmon in both lakes from spring to fall is likely a result of the enhanced activity of those salmon smoltifying in the spring (Ruggles 1980; Wedemeyer et al. 1980), which increased their susceptibility to capture by passive gear at that time.

Salmon were easier to catch in the spring and more difficult to catch in the fall than trout. As a result, CPUE could not be used as a simple index of the relative abundance of the two species within or between lakes. Comparisons of this nature would require compensation for differing catchabilities, as has been found with other types of passive gear and other fish communities (Craig 1980). The equations derived here are likely applicable for this purpose to other small salmonid lakes, at least in central Newfoundland.

Acknowledgments

L. J. Cole and D. P. Riche assisted with data collection and G. Marshall assisted with statistical analysis. S. Gavaris provided an informative explanation on comparisons of catchability. W. J. Bruce, Dr R. J. Gibson, and Dr J. H. C. Pippy constructively reviewed the manuscript.

References

CHADWICK, E. M. P. 1982. Stock-recruitment relationship for Atlantic salmon (*Salmo salar*) in Newfoundland rivers. Can. J. Fish. Aquat. Sci. 39: 1496–1501.

CRAIG, J. F. 1980. Sampling with traps, p. 55–70. *In* T. Backiel and R. L. Welcomme [ed.] Guidelines for sampling fish in inland waters. EIFAC Tech. Pap. 33: 176 p.

DIXON, W. J., AND F. J. MASSEY JR. 1969. Introduction to statistical analysis. 3rd ed. McGraw-Hill Publications, New York, NY. 638 p.

POWER, G. 1980. The brook charr, *Salvelinus fontinalis*, p. 141–203. *In* E. K. Balon [ed.] Charrs: salmonid fishes of the genus *Salvelinus*. Dr. W. Junk bv Publishers, The Hague, Netherlands.

RICKER, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191: 382 p.

RUGGLES, C. P. 1980. A review of the downstream migration of Atlantic salmon. Can. Tech. Rep. Fish. Aquat. Sci. 952: ix + 39 p.

RYAN, P. M. 1982. Species composition and seasonal abundance of zooplankton in the Experimental Ponds Area, central Newfoundland, 1977–80. Can. Data Rep. Fish. Aquat. Sci. 318: iv + 85 p.

SCOTT, W. B., AND E. J. CROSSMAN. 1964. Fishes occurring in the fresh waters of insular Newfoundland. Dep. Fish. Ottawa. 124 p.

WEDEMEYER, G. A., R. L. SAUNDERS, AND W. C. CLARKE. 1980. Environmental factors affecting smoltification and early marine survival of anadromous salmonids. Mar. Fish. Rev. 42(6): 1–14.

An Improved Flow-through Respirometer for Aquatic Macroinvertebrate Bioenergetic Research

Frederick J. Wrona and Ronald W. Davies

Department of Biology, University of Calgary, Calgary, Alta. T2N 1N4

Wrona, F. J., and R. W. Davies. 1984. An improved flow-through respirometer for aquatic macroinvertebrate bioenergetic research. Can. J. Fish. Aquat. Sci. 41: 380–385.

An improved flow-through respirometer that is simple to construct and operate is described. Using an impedance monitoring system, activity-specific aerobic metabolism of macroinvertebrates can be quantified under controlled temperatures and oxygen tensions. Application of the respirometer is demonstrated by examining the activity-specific respiratory responses of two species of Hirudinoidea to 100% air-saturated conditions and differing levels of hypoxia. Acclimation time of the animals to the respirometer chambers is also investigated. Using this type of flow-through system for macroinvertebrate bioenergetic studies, activity-specific respiration measurements can be made under constant abiotic conditions and minimal disturbance to the animals.

On décrit un respiromètre «à débit continu» ("flow-through") perfectionné qui est simple à construire et à utiliser. Au moyen d'un système de contrôle par impédance, le métabolisme aérobie pour certaines activités de macroinvertébrés peut être quantifié dans des conditions de température et de pression d'oxygène contrôlées. L'application du respiromètre est démontrée par l'examen des réponses respiratoires pour certaines activités de deux espèces d'hirudinés soumises à des conditions de 100 % d'air saturé et à différents niveaux d'hypoxie. On étudie également le temps d'acclimatation des animaux aux chambres du respiromètre. En utilisant ce type de système à débit continu pour des études bioénergétiques sur les macroinvertébrés, on peut prendre des mesures sur la respiration pour certaines activités, dans des conditions abiotiques constantes et en dérangeant le moins possible les animaux.

Received June 27, 1983
Accepted October 13, 1983

Reçu le 27 juin 1983
Accepté le 13 octobre 1983

The energy expenditure (metabolism) of aquatic organisms has most commonly been indirectly quantified by measuring respiration. Aquatic ecologists have used two types of respirometers to quantify oxygen uptake of macroinvertebrates: closed and flow-through systems.

Closed respirometers are based on the principle of measuring the oxygen depletion of the water in a sealed chamber using chemical, manometric, or polarographic techniques. Pattee (1962), Kamler (1969), Rueger et al. (1969), Lawton and Richards (1970), and Teal (1971) provide detailed comparisons of a number of closed respirometers, although the closed-bottle and the manometric based Gilson (1963) systems have been the most commonly used in aquatic bioenergetic research. There are many problems associated with the use of closed respirometers for quantifying oxygen uptake, the most severe being that the respiration rates of the organisms are being measured under progressively increasing hypoxia and metabolic waste accumulation (Mann 1958; Kamler 1969; Rueger et al. 1969; Nagell 1975). Both of these environmental factors are potentially stressful and will affect the measured rate of respiration (Rueger et al. 1969; Kamler 1969).

Flow-through polarographic respirometers were developed (Mann 1958; Bielowski 1959, 1961; Edwards and Learner 1960; Klekowski and Kamler 1968, 1971; Rueger et al. 1969; Nagell 1975) for use on macroinvertebrates in an attempt to alleviate some of the problems associated with closed systems by providing a constant oxygen tension to the test organism while continuously removing metabolites. Although flow-through respirometers offered obvious advantages over static systems, their implementation in aquatic bioenergetic research has been limited. Difficulty in calibration (Mann 1958; Bielowski 1959, 1961; Berg and Jónasson 1965; Nagell 1975) and complexity in construction and operation (Edwards and Learner 1960; Klekowski and Kamler 1968, 1971; Rueger et al. 1969) have probably been the major factors most responsible for precluding their general use.

An additional serious limitation of previously designed static and flow-through respirometers has been the inability to quantify accurately the activity patterns of an organism concurrently with the measurement of respiration. Since activity greatly influences oxygen uptake (Bennett 1978), quantification of the levels of activity is essential to determine whether the respiration measurements are truly indicative of standard, routine, or active metabolism (Prosser and Brown 1962).

This paper presents an improved flow-through respirometer that is simple to construct and to operate, measures respiration rates under controlled temperature and oxygen tensions, and allows for concurrent monitoring of activity patterns of the test organism so that activity-specific respiration rates can be determined.

Materials and Methods

Respirometer construction — Figure 1 is a schematic representation of the respirometer system. Water of known oxygen concentration and temperature is delivered to the respiration chambers from an outlet located at the bottom of a styrofoam-insulated reservoir (20-L Nalgene carboy). Water temperature in the reservoir is regulated using an Instant Ocean refrigeration–recirculating system (model WM 500), which also biologically filters the water through fine gravel. Filtered water is pumped into the reservoir where a constant level of water is maintained by an overflow outlet installed near the top of the unit.

Oxygen tension of the water in the reservoir is controlled by bubbling with either compressed air or nitrogen through airstones located on the bottom of the reservoir. Air-saturated (100%) water is achieved by bubbling violently with compressed air. Hypoxic water of known oxygen saturation is produced by adjusting the volume of nitrogen entering the reservoir, which strips away the oxygen of the incoming water. The volume of nitrogen required to maintain a preset level of hypoxia is automatically metered using a Radiometer Tox-40 gas transmitter coupled to a Radiometer CME 40 on/off controller (McMahon et al. 1978). An oxygen electrode (Radiometer E51443/o) connected to the gas transmitter continuously monitors the oxygen tension of the outflow water enroute to the respirometer chambers. If the oxygen tension deviates (± 5 torr = 666.6 Pa) from the present level on the CME 40 controller, a solenoid valve regulates nitrogen delivery by automatically opening or closing.

Modified 2- or 5-mL glass syringes constitute the respiration chambers, all of which are housed in a light-proof, styrofoam-insulating water jacket that keeps the chambers in the dark and at the same temperature as the experimental input water. Twelve chambers are used, 10 experimental and 2 controls. The volume of the syringes used is dependent on the size of the test organisms. The flow rate of the water through each respirometer chamber (0.2–0.8 mL·min^{-1}) is individually controlled with pinch valves located on each Tygon tubing input line (Travenol blood collection sets with Flo-Trol clamps). Improved flow control is achieved when the water feed lines to the respirometers are regulated using a 12-channel, variable-speed peristaltic pump (Manostat Cassette pump).

Each respirometer chamber is fitted with two electrodes (0.05-mm^2 copper magnet wire bared of insulation for 1 cm),

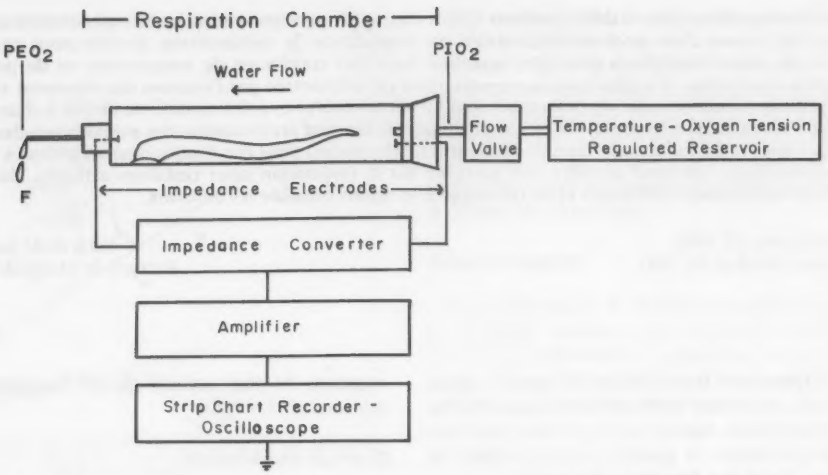


FIG. 1. Schematic representation of respiration apparatus (see text for explanation of symbols).

one at each end. Fine-mesh plastic gauze is placed over the electrodes so that the animal in the chamber can not directly contact them. Activity of the test organism in each chamber is monitored by connecting the appropriate two electrodes to a Biocom 2991 impedance converter. The converter generates a low oscillating current between the electrodes, with the water inside the respirometer acting as the electron carrier completing the circuit. Any movement of the animal inside the chamber produces a change in the impedance of the circuit, which is amplified by the converter and a Grass P15 A.C. preamplifier. The P15 amplifier also has built-in frequency filters that can be adjusted to produce a clean signal from the respirometers. The signal is displayed on an oscilloscope and/or strip chart recorder. Thus, animal activity is observed as either beam movement on the oscilloscope screen or is permanently recorded on the strip chart recorder.

Respirometer operation — Weight-specific oxygen uptake of the test animal was calculated using the relationship (after Wilkes and McMahon 1982)

$$\dot{M}_{O_2} = \frac{(P_{I_{O_2}} - P_{E_{O_2}})(\alpha_{O_2})(F)}{wt}$$

where $\dot{M}_{O_2}$ = rate of oxygen consumption ($\mu mol \cdot mg^{-1} \cdot h^{-1}$), $P_{I_{O_2}}$ = partial pressure of oxygen of incoming water (torr), $P_{E_{O_2}}$ = partial pressure of oxygen of exiting water (torr), α_{O_2} = solubility coefficient of oxygen in water at a defined temperature ($\mu mol \cdot L^{-1} \cdot torr^{-1}$) (from Dejours 1975), F = flow rate of water through respirometer chamber ($L \cdot h^{-1}$), and wt = wet or dry weight of individual (mg).

The oxygen tensions of the water ($P_{I_{O_2}}$, $P_{E_{O_2}}$) are obtained by taking 100-μL samples using a 250-μL microsyringe and injecting the sample into a Radiometer oxygen electrode (E5046), which is housed in a thermostatic glass jacket (Radiometer D616). $P_{I_{O_2}}$ is obtained by taking a sample from the control chamber that contains no animal. The thermostatic jacket keeps the electrode at the same temperature as the experimental water. The partial pressure of oxygen is directly measured in torr (1 torr = 133.322 Pa) using a Radiometer PHM 73 digital gas monitor (accuracy ±4 torr). A stable reading is usually achieved within 2 min. The flow rate of water through the respirometers (F) is determined on each individual chamber at the time the oxygen readings are taken. A 5-mL volumetric pipette, with its tip sealed (accuracy ±0.05 mL), is used to collect the exiting water from the chamber for a 1-min interval. The flow rate of the water through each respirometer is always adjusted so that a minimum of 5 torr difference is obtained between the $P_{I_{O_2}}$ and $P_{E_{O_2}}$ readings for the given experimental conditions. Oxygen consumption of the animals may be converted to a volumetric rate (standardized to STPD) using

$$\dot{V}_{O_2} = (\dot{M}_{O_2})(22.414\ L \cdot mol^{-1})$$

where $\dot{V}_{O_2}$ = rate of oxygen consumption ($\mu L \cdot mg^{-1} \cdot h^{-1}$). Between experimental runs the respirometers should be cleaned with 95% ethanol to prevent bacterial buildup.

Respirometer application — The respirometer system was tested using adult, nonreproductive *Nephelopsis obscura* and *Erpobdella punctata* (Hirudinoidea: Erpobdellidae). Upon collection (November), the leeches were acclimated in the laboratory to the test temperature (15°C) and starved for 28 d. Similar wet weight ranges (150–400 mg) of both species were used. Ten individuals of each species were tested, with five replicate respiration readings taken per individual. The activity of an individual was observed for a sufficient period of time immediately prior and also during the actual measurement of oxygen uptake to ensure that the respiration reading was indicative of a specific activity pattern. This time period was standardized to one complete change of water within the respirometer chamber.

The time required for each species to become acclimated to the test conditions in the respiration chambers was also determined. Respiration readings of quiescent animals under 100% air-saturated conditions were taken at 6-, 12-, 24-, 48-, and 72-h intervals after placement in the respirometers. A model I, one-way ANOVA (Zar 1974) was used to test for time-related differences in oxygen uptake. Hypothesis testing was performed at the $P = 0.05$ level of probability.

The effects of hypoxia on the respiration rates of *N. obscura* and *E. punctata* were examined by measuring the oxygen uptake of both species under progressively declining oxygen tensions at each of 100, 50, 25, and 10% air saturation. Experiments were begun at 100% air saturation and the same group of animals were kept for 2 h at each oxygen tension level.

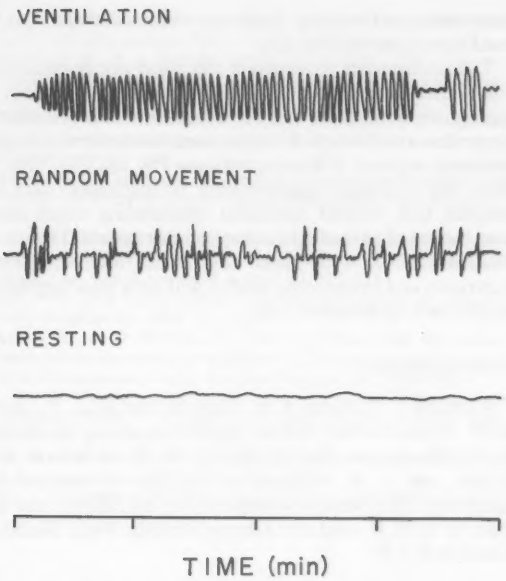


FIG. 2. Impedance recordings of locomotory movements displayed by *N. obscura* and *E. punctata* during respiration analyses.

The animals were gradually exposed over a 1-h period to the next lower concentration.

Results

Three activity states were defined for *N. obscura* and *E. punctata* using the impedance monitoring system. These were (1) ventilation: rhythmic dorsal–ventral undulations of the body while maintaining the posterior sucker attached (Fig. 2a), (2) random movement: associated with crawling, short bursts of swimming, and random probing by the leeches' anterior (Fig. 2b), and (3) resting: no measurable activity (Fig. 2c).

No measurements of quiescent metabolism were obtained for either species when readings were taken 1 h after the animals were placed in the respirometers (Table 1). However, one-way ANOVA showed no significant time-related differences in quiescent respiration rates for either *N. obscura* or *E. punctata* when readings were taken at intervals between 6 and 72 h in the respirometers (Table 1).

No significant differences were found in oxygen consumption for either species between individuals displaying random movement or ventilation (Table 2). However, under 100% air-saturated conditions, a Student *t*-test showed the respiration rates for active (randomly moving or ventilating) *N. obscura* and *E. punctata* to be significantly higher than obtained for resting individuals.

TABLE 1. Mean quiescent oxygen uptake rates ($\dot{V}_{O_2}$) ($\mu L \cdot mg$ dry $wt^{-1} \cdot h^{-1}$ ± SE) of starved, nonreproductive *N. obscura* and *E. punctata* taken at a number of intervals over a 72-h period after initial placement in the respirometer chambers.

Time in respirometer (h)	*N. obscura*	*E. punctata*
1	—	—
6	0.20±0.03	0.29±0.02
12	0.17±0.02	0.26±0.01
24	0.22±0.02	0.28±0.03
48	0.21±0.01	0.28±0.02
72	0.19±0.01	0.30±0.02

TABLE 2. Mean oxygen uptake rates ($\dot{V}_{O_2}$) ($\mu L \cdot mg$ dry $wt^{-1} \cdot h^{-1}$ ± SE) of starved, nonreproductive *N. obscura* and *E. punctata* under different activity patterns when exposed to 100% air-saturated conditions and progressively increasing hypoxia at 15°C.

% air saturation	Resting	Random movement	Ventilating
N. obscura			
100	0.21±0.02	0.54±0.09	0.52±0.10
50	0.04±0.01	0.36±0.05	0.32±0.04
25	0.03±0.01	0.18±0.01	0.10±0.07
10	0.02±0.01	0.03±0.01	0.03±0.02
E. punctata			
100	0.27±0.02	0.59±0.11	0.54±0.09
50	0.05±0.01	0.35±0.07	0.55±0.05
25	0.03±0.01	0.13±0.04	0.20±0.03
10	0.02±0.01	0.06±0.01	0.04±0.01

In response to short-term hypoxia, quiescent *N. obscura* and *E. punctata* displayed similar trends with their oxygen uptake rates correspondingly declining with the lowering of oxygen tension. Randomly moving and ventilating individuals also displayed the same type of oxyconformity (Prosser and Brown 1962), although their respiration rates were higher than obtained for resting animals (Table 2).

Discussion

Since respiration rates of aquatic macroinvertebrates are influenced by many physiological and environmental factors (Dejours 1975; Weber 1978; Wells 1980), consideration must be made with respect to the type of respirometer system used to quantify aerobic metabolism. Many respirometers, especially closed systems, usually provide inadequate controls or measures for factors, such as activity levels, oxygen availability, and physiological stress, or themselves introduce extraneous variables that potentially alter the normal respiratory pattern of an animal.

Despite criticisms (Mann 1958; Kamler 1969), the closed-bottle respirometer has been widely used in aquatic respiration research (e.g. Berg et al. 1962; Eriksen 1963, 1964; Lawton 1971; Otto 1974; Calow 1975; Nilsson 1974; Sweeney 1978), probably because it is a simple system to construct and operate. Kamler (1969) criticized the closed-bottle technique on the grounds that (1) environmental conditions were not constant during the experimental period (i.e. decreasing oxygen tension and increasing metabolites), (2) oxygen gradients formed as a result of water stagnation, which stressed the animals and induced elevated activity, and (3) inconsistent respiration readings were obtained in relation to the duration time of the experiment. Criticism 2 can be overcome if the duration of the experiment is standardized; however, problems still arise if intra- and inter-specific comparisons are to made between studies using different experimental periods. Some researchers have attempted to overcome criticism 2 by using closed-bottle systems with stirring mechanisms installed (Nilsson 1974; Otto 1974; Sweeney 1978), but this only overcomes the problem if

the stirring mechanism does not itself disturb the organism. More importantly, the closed-bottle system is only a suitable technique if the intent of the study is to examine the effects of the phenomenon of oxygen depletion on invertebrate respiratory responses, as illustrated by Mangum and Van Winkle (1973). However, adequate precautions must still be taken to control the problems associated with metabolite accumulation (criticism 1).

Gilson's (1963) manometric respirometer has also been widely used in macroinvertebrate respiration studies (e.g. Knight and Gaufin 1966; Sweeney and Schnack 1977; Vannote 1978; Sweeney 1978; Osborne et al. 1980; Sweeney and Vannote 1981; Linton et al. 1982). In addition to having similar problems as the closed-bottle system, the Gilson respirometer produces an even more unnatural, disturbed environment for the test animal by requiring the chambers to be shaken to eliminate gas stratification (Rueger et al. 1969; Nagell 1975). The mechanical agitation coupled with some models having bright flood lamps to illuminate the manometers when readings are taken is potentially stress inducing. Hence, due to its many inherent problems, the Gilson respirometer is generally not a suitable system for macroinvertebrate bioenergetic studies (Nagell 1975).

A problem associated with previous static and flow-through respirometers has been the inability to determine quantitatively whether the measured oxygen uptake rates were indicative of standard, routine, or active metabolism. By design, it is impossible to observe animal activity directly when using the Gilson respirometer. Similarly, when using other types of respirometers, the chambers are usually covered to minimize disturbances to the test animals. Hence, either assumptions are made with respect to the type of metabolism being measured (e.g. Berg and Jónasson 1965; Calow 1975; Sweeney and Vannote 1981) or direct observations of activity are made on uncovered chambers, which are then correlated with the measured levels of oxygen uptake (e.g. Knight and Gaufin 1966; Nagell 1973).

The flow-through respirometer presented in this paper overcomes all of the discussed criticisms associated with previous systems. By using the impedance monitoring feature, it was possible to define three states of activity (resting, random movement, ventilation) while the animals were kept in constant darkness so as to minimize extraneous disturbances. Using the derived movement patterns, it was possible to quantify activity-specific respiration rates for both species when exposed to different oxygen tensions. Osborne et al. (1980) and Linton et al. (1982) used a Gilson respirometer and reported significantly higher respiration rates for *N. obscura* and *E. punctata* under 100% air-saturated conditions at 15°C than obtained for resting and active individuals in this study. This difference is probably illustrative of the Gilson respirometer quantifying the aerobic metabolism of stressed animals.

Acclimation time to the experimental conditions in the respirometer is also critical to obtain meaningful respiration measurements (Kamler 1969; McMahon et al. 1974). The main advantage of using a flow-through system is that constant abiotic environmental conditions can be maintained for a sufficient time to allow acclimation (Kamler 1969). Using the impedance system, we found that after only 1 h in the respirometers neither *N. obscura* nor *E. punctata* were quiescent (Table 1). Beyond 6 h in the respiration chambers, it was possible to obtain measurements of resting metabolism for both species, and these rates did not significantly change over the remaining 72-h experimental period (Table 1). This stability in respiratory performance indicates that acclimation to test conditions occurred after 6 h.

The respirometer presented in this paper can be applied to a wide variety of lentic and lotic macroinvertebrates by selecting appropriate syringe sizes for the chambers and determining the proper flow rate through the respirometers to achieve at least the minimum required difference between $P_{I_{O_2}}$ and $P_{E_{O_2}}$ (Fig. 1). Since the ecological interpretation of respiration data is a complex task without additional confounding errors arising from the use of an inadequate respirometer system (Lawton and Richards 1970), it is hoped that future macroinvertebrate respiration and bioenergetic studies will use a more appropriate system such as described here.

Acknowledgments

We thank C. E. Booth, J. M. Culp, D. Iredale, L. R. Linton, and P. Wilkes for their helpful suggestions during the development of the system. Special thanks to B. R. McMahon, R. L. Walker, and J. R. Wilkens for the use of some of their equipment. This work was supported by an NSERC operating grant to R.W.D. and an Alberta Heritage Fund Steinhauer Award to F.J.W.

References

Bennett, A. F. 1978. Activity metabolism of lower invertebrates. Annu. Rev. Physiol. 400: 447–469.

Berg, K., and P. M. Jónasson. 1965. Oxygen consumption of profundal lake animals at low oxygen content of the water. Hydrobiologia 26: 131–143.

Berg, K., P. M. Jónasson, and K. W. Ockelmann. 1962. The respiration of some animals from the profundal zone of a lake. Hydrobiologia 19: 1–39.

Bielowski, J. 1959. A polarographic method of measuring the intensity of respiration of aquatic animals. Acta Biol. Exp. 19: 41–48.

1961. The use of a solid platinum electrode for continuous recording of the rate of respiration. Comp. Biochem. Physiol. 3: 261–266.

Calow, P. 1975. The respiratory strategies of two species of freshwater gastropods (*Ancylus fluviatilis* Müll. and *Planorbis contortus* Linn.) in relation to temperature, oxygen concentration, body size, and season. Physiol. Zool. 48: 114–129.

Dejours, P. 1975. Principles of comparative respiratory physiology. American Elservier Publ. Co., New York, NY.

Edwards, R. W., and M. A. Learner. 1960. Some factors affecting the oxygen consumption of *Asellus*. J. Exp. Biol. 37: 706–718.

Eriksen, C. H. 1963. The relation of oxygen consumption to substrate particle size in two burrowing mayflies. J. Exp. Biol. 40: 447–453.

1964. The influence of respiration and substrate upon the distribution of burrowing mayfly naiads. Verh. Int. Ver. Limnol. 15: 903–911.

Gilson, W. E. 1963. Differential respirometer of simplified and improved design. Science (Washington, DC) 141: 531–532.

Kamler, E. 1969. A comparison of the close-bottle and flowing-water methods for measurement of respiration in aquatic invertebrates. Pol. Arch. Hydrobiol. 16: 31–49.

Klekowski, R. Z., and E. Kamler. 1968. Flowing water polarographic respirometer for aquatic animals. Pol. Arch. Hydrobiol. 15: 121–144.

1971. Flowing water polarographic respirometer, p. 280–287. *In* W. T. Edmundson and G. G. Winberg [ed.] A manual on methods for the assessment of secondary productivity in freshwaters. IBP Handbook No. 17. Blackwell Scientific Publications, Oxford.

Knight, A. W., and A. R. Gaufin. 1966. Oxygen consumption of several species of stoneflies (Plecoptera). J. Insect Physiol. 12: 347–355.

Lawton, J. H. 1971. Ecological energetics studies on larvae of the damselfly *Pyrrhosoma nymphula* (Sulzer) (Odonata: Zygoptera). J. Anim. Ecol. 40: 385–423.

Lawton, J. H., and J. Richards. 1970. Comparability of Cartesian, Diver, Gilson, Warburg and Winkler methods of measuring the respiratory rates of aquatic invertebrates in ecological studies. Oecologia 4: 319–324.

Linton, L. R., R. W. Davies, and F. J. Wrona. 1982. Osmotic and respirometric responses of two species of Hirudinoidea to changes in water chemistry. Comp. Biochem. Physiol. 71A: 243–247.

Mangum, C. P., and W. Van Winkle. 1973. Responses of aquatic invertebrates to declining oxygen conditions. Am. Zool. 13: 529–541.

MANN, K. H. 1958. Seasonal variation in the respiratory acclimatization in the leech *Erpobdella testacea* (Sav.). J. Exp. Biol. 35: 314–323.

MCMAHON, B. R., P. J. BUTLER, AND E. W. TAYLOR. 1978. Acid–base changes during recovery from disturbance and during long term hypoxic exposure in the lobster *Homarus vulgaris*. J. Exp. Zool. 205: 361–370.

MCMAHON, B. R., W. W. BURGGREN, AND J. L. WILKENS. 1974. Respiratory responses to long-term hypoxic stress in the crayfish *Orconectes virilis*. J. Exp. Biol. 60: 195–206.

NAGELL, B. 1973. The oxygen consumption of mayfly (Ephemeroptera) and stonefly (Plecoptera) at different oxygen concentration. Hydrobiologia 42: 461–489.

1975. The open-flow respirometric method: precision of measurement in general and description of a high precision respirometer for aquatic animals. Int. Rev. Gesamten Hydrobiol. 60: 655–667.

NILSSON, L. M. 1974. Energy budget of a laboratory population of *Gammarus pulex* (Amphipoda). Oikos 25: 35–42.

OSBORNE, L. L., R. W. DAVIES, AND J. B. RASMUSSEN. 1980. The effect of total residual chlorine on the respiration rates of two species of freshwater leech (Hirudinoidea). Comp. Biochem. Physiol. 67(C): 203–205.

OTTO, C. 1974. Growth and energetics in a larval population of *Potamophylax cingulatus* (Steph.) (Trichoptera) in a south Swedish stream. J. Anim. Ecol. 43(2): 339–361.

PATTEE, E. 1962. Méthodes de mesure du métabolisme respiratoire chez les animaux aquatiques. Hydrobiologia 19: 40–56.

PROSSER, C. L., AND F. A. BROWN. 1962. Comparative animal physiology. W. B. Saunders Co., London.

RUEGER, M. E., T. A. OLSON, AND J. I. SCOFIELD. 1969. Oxygen requirements of benthic insects as determined by manometric and polarographic techniques. Water Res. 3: 99–120.

SWEENEY, B. W. 1978. Bioenergetic and developmental response of a mayfly to thermal variation. Limnol. Oceanogr. 23: 461–477.

SWEENEY, B. W., AND J. A. SCHNACK. 1977. Egg development, growth, and metabolism of *Sigara alternata* (Say) (Hemiptera: Corixidae) in fluctuating thermal environments. Ecology 58: 265–277.

SWEENEY, B. W., AND R. L. VANNOTE. 1981. *Ephemerella* mayflies of White Clay Creek: bioenergetic and ecological relationships among six coexisting species. Ecology 62: 1353–1369.

TEAL, J. M. 1971. Respiration and energy flow, p. 270–276. *In* W. T. Edmundson and G. G. Winberg [ed.] A manual on methods for the assessment of secondary productivity in fresh waters. IBP Handbook No. 17. Blackwell Scientific Publications, Oxford.

VANNOTE, R. L. 1978. A geometric model describing a quasi-equilibrium of energy flow in populations of stream insects. Proc. Natl. Acad. Sci. U.S.A. 75: 381–384.

WEBER, R. E. 1978. Respiration. *In* P. J. Mill [ed.] Physiology of annelids. Academic Press Inc., Ltd., London.

WELLS, R. M. G. 1980. Invertebrate respiration. The Institute of Biology's Studies in Biology No. 127. Edward Arnold (Publishers) Ltd., London.

WILKES, P. R. H., AND B. R. MCMAHON. 1982. Effect of maintained hypoxic exposure on the crayfish *Orconectes rusticus*. I. Ventilatory, acid-base and cardiovascular adjustments. J. Exp. Biol. 98: 119–137.

ZAR, J. H. 1974. Biostatistical analysis. Prentice-Hall, Inc., Toronto, Ont.

Ethanol Fractionation of Lacustrine Colloidal Fibrils

B. Kent Burnison and Gary G. Leppard

Aquatic Ecology Division, National Water Research Institute, Box 5050, Burlington, Ont. L7R 4A6

Burnison, B. K., and G. G. Leppard. 1984. Ethanol fractionation of lacustrine colloidal fibrils. Can. J. Fish. Aquat. Sci. 41: 385–388.

Ethanol fractionation of colloidal organic fibrils can provide a highly purified fraction in appropriate quantities for standard chemical analyses of fibril structure and function. Using a sequential ethanol precipitation procedure, applied to lacustrine fibrils isolated and concentrated by physical separation techniques, we obtained a fibril fraction (approximately 60% yield). Its characteristics were as follows: (1) absence of any major category of colloidal impurity detectable by transmission electron microscopy, (2) relative freedom from fibrils of atypical morphology, (3) relative freedom from a class of small granules, typically associated with lacustrine fibrils and with some other kinds of polyanionic fibrillar colloids found in nature, (4) freedom from derivatization reactions, and (5) freedom from an undesirable exposure to caustic reagents. Our objective was to arrive at a nondegradative fractionation procedure that yielded a fraction relatively free of other colloidal components found in lake water. This fraction would then be appropriate for assays of heavy metal binding and bioavailability.

Le fractionnement à l'éthanol de fibrilles organiques colloïdales peut fournir une fraction de fibrilles très purifiée en quantités suffisantes pour des analyses chimiques standard de la structure et de la fonction de ces fibrilles. À l'aide d'une méthode de précipitation séquentielle à l'éthanol, appliquée à des fibrilles lacustres isolées et concentrées par des méthodes de séparation physiques, nous avons obtenu une fraction de fibrilles (rendement d'environ 60 %). Ses caractéristiques sont les suivantes : (1) libre de toute catégorie majeure d'impuretés colloïdales détectables par microscopie électronique à transmission, (2) relativement libre des fibrilles de morphologie atypique, (3) relativement libre d'une classe de petits granules, typiquement associés aux fibrilles lacustres, et à certains genres de colloïdes fibrillaires polyanioniques trouvés dans la nature, (4) libre de réactions de dérivations et (5) libre d'une exposition indésirable à des réactifs caustiques. On avait comme objectif d'en arriver à une méthode de fractionnement non dégradable donnant une fraction relativement libre d'autres éléments colloïdaux présents dans l'eau des lacs. Cette fraction pourrait alors servir à des analyses de fixation et de bioaccessibilité des métaux lourds.

Received August 3, 1983
Accepted November 18, 1983

Reçu le 3 août 1983
Accepté le 18 novembre 1983

A colloid fraction, highly enriched for organic "fibrils" (Leppard et al. 1977), can be isolated routinely from lake water using physical separation techniques (Burnison and Leppard 1983). Polysaccharide is the main chemical constituent of these organic fibrils (Burnison 1978). In our earlier work, we did not attempt any chemical fractionation of the physically isolated high molecular weight materials, but the utility of a mild purification procedure was evident. Ethanol is commonly used to fractionate carbohydrate polymers (Whistler and Sannella 1965), and in the case of mucopolysaccharides, ethanol precipitation is done usually in the presence of Na, K, Ca, Ba, Cd, or Zn salts (Jeanloz 1970). We chose to develop a purification procedure based on ethanol and a sodium salt, bearing in mind the recent work of Ghosh and Schnitzer (1980). Using electron microscopic monitoring of experiments with soil humic and fulvic acids, they were able to show a transition between a fibrous state (flexible linear colloid) and a globular state (rigid spherocolloid), which depended on physicochemical variables such as sample concentration, pH, and neutral electrolyte concentration.

From the physicochemical nature of the fibrils and the quantities that can be present we suggest that they have roles in the modulation of lacustrine physiological processes (Leppard and Burnison 1983). With the intent of delineating some roles, we report here a biochemical fractionation procedure designed to produce a uniform fibril fraction of high yield and purity. This procedure is based on selective precipitation by a noncaustic reagent (ethanol) and it provides the analyst with essentially one morphological type of lacustrine fibril for refined chemical analyses.

Methods

Offshore epilimnetic water from St. George Lake, near Toronto, Ont. (43°57′30″N, 79°25′30″W), was sampled and processed as described by Burnison and Leppard (1983) using a physical separation scheme for isolating and concentrating a colloidal fibril-rich fraction. We experimented on freshly isolated fibril-rich fractions using a variety of gentle fractionation techniques to obtain a more uniform preparation than had been achieved previously. The procedure of choice is described in Fig. 1 and is related to the physical isolation scheme. The monitoring at all fractionation steps by optical microscopy and transmission electron microscopy (TEM) was carried out according to Burnison and Leppard (1983). TEM observations and photographs were made with a Philips 300 electron microscope. Each ethanolic (EtOH) precipitate, after dialysis against distilled water, and the final supernatant were freeze-

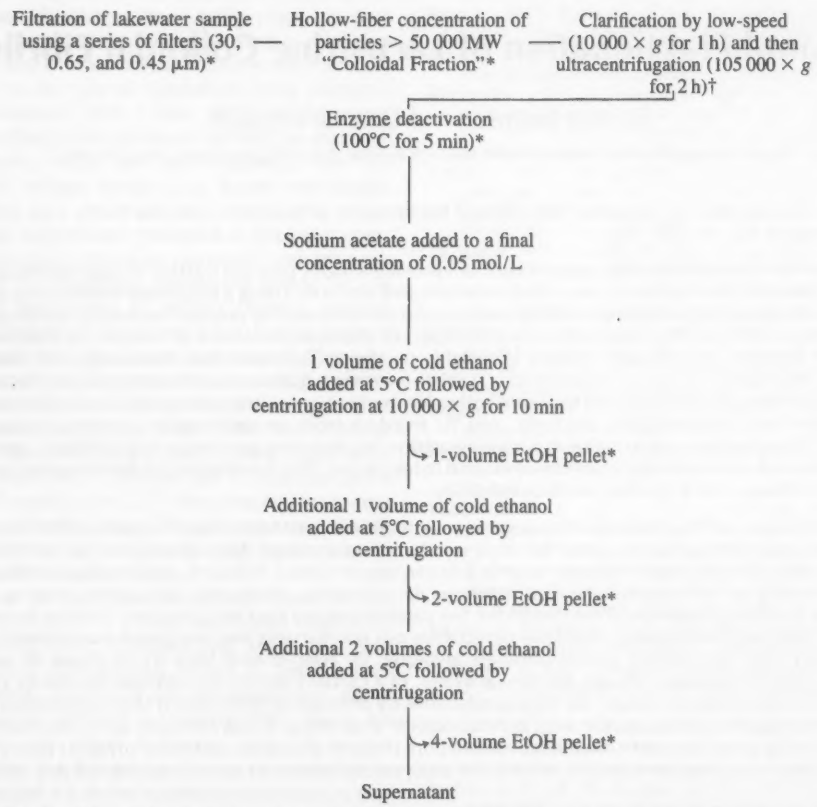

Filtration of lakewater sample using a series of filters (30, 0.65, and 0.45 μm)*
Hollow-fiber concentration of particles > 50 000 MW "Colloidal Fraction"*
Clarification by low-speed (10 000 × g for 1 h) and then ultracentrifugation (105 000 × g for 2 h)†
Enzyme deactivation (100°C for 5 min)*
Sodium acetate added to a final concentration of 0.05 mol/L
1 volume of cold ethanol added at 5°C followed by centrifugation at 10 000 × g for 10 min
1-volume EtOH pellet*
Additional 1 volume of cold ethanol added at 5°C followed by centrifugation
2-volume EtOH pellet*
Additional 2 volumes of cold ethanol added at 5°C followed by centrifugation
4-volume EtOH pellet*
Supernatant

FIG. 1. Ethanol fractionation procedure for colloidal fibrils. *Observed by transmission electron microscopy. †Clarification step removed a pellet of coarse materials (i.e. cell membranes) negligible in quantity.

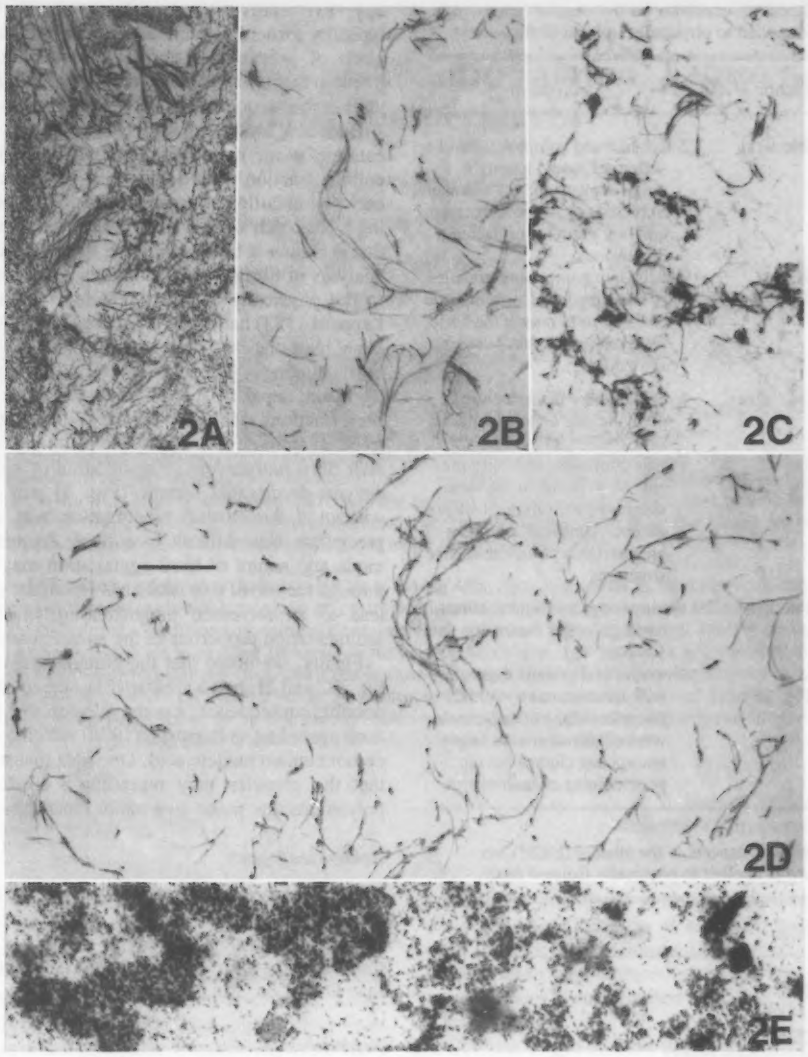


FIG. 2. Effectiveness of ethanol fractionation in yielding a uniform fibril fraction of high purity. (A) Fibrils of the physically isolated fraction after enzyme deactivation; (B) principal component of the 1-volume EtOH pellet; (C) some of its granular contaminants and atypical fibrils; (D) desired fraction, the 2-volume EtOH pellet; (E) 4-volume EtOH pellet, which contains the major mass of granular contaminants. Bar = 0.45 μm.

dried; we compared the dry weights with the dry weight of an unfractionated control sample. We used these weights to calculate the yield per fraction and to serve as a check on procedural losses.

Results

Morphological observations on the selectivity of the ethanolic precipitation steps are given in Table 1. The effectiveness of the fractionation, as determined visually, is illustrated in Fig. 2. All of the monitoring steps not described here gave results essentially identical to those previously published for the physical separation scheme (Burnison and Leppard 1983). This indicates a high yield and quality of the fresh fibril-rich fractions used as a starting material for the ethanol fractionation we describe. The starting material was extremely enriched in fibrils (Fig. 2A, 2B); its defects resided mainly in the presence of granules of ribosomal dimensions and in the presence of small groups of fibrils of unusual physical dimensions (Fig. 2C). The increases in purity and uniformity achieved over the best previous effort is illustrated in Fig. 2D (compare with Fig. 7 and 8 of Burnison and Leppard 1983). The nature of the principal contaminants, the well-stained granules and some weakly stained clumps of amorphous material, is shown in Fig. 2E. To see the qualitative findings from TEM in a quantitative context, see Table 2, which presents a dry weight analysis of fractions

TABLE 1. Morphological observations on the ethanol (EtOH) fractionation procedure as applied to physically isolated fibrils.

Fraction	Resolution level	Description
1-volume EtOH pellet	Visible light	Sheet-like and complex tube-like structures, some having a major dimension > 100 μm. Some coarse fibrous structures and tiny granules of bacterial dimensions
	TEM (Fig. 2B, 2C)	Fibrils dominant, many granules of ribosomal dimensions, little else present. Many of the fibrils were extremely thin but some were coarse
2-volume EtOH pellet	Visible light	Irregular sheet-like structures, many having a major dimension > 100 μm
	TEM (Fig. 2D)	Fibrils dominant, little else present. Most fibrils in the same size range with atypical shapes absent. Almost all fibrils aggregated into porous sheet-like structures
4-volume EtOH pellet	Visible light	Grainy irregular chunks, some having a major dimension > 100 μm
	TEM (Fig. 2E)	Granules and granule aggregates with most granules < 0.025 μm wide. Many of the granules were clustered around larger amorphous clumps having poor staining characteristics

TABLE 2. Quantitative aspects of the ethanol (EtOH) fractionation procedure as applied to physically isolated fibrils.

Fraction	Dry weight of fraction[a]
1-volume EtOH pellet	14
2-volume EtOH pellet	58
4-volume EtOH pellet	20
Supernatant (from 4-volume pellet)	8

[a]Weight is expressed as a percentage of total recovered material. The procedural loss came to 4% as compared with the unfractionated control (enzyme-deactivated sample).

derived from St. George Lake. Note that the 2-volume EtOH pellet illustrated in Fig. 2D represents 58% of the total recoverable material. This in turn represented 96% of the starting material, which contained 30% of the total organic carbon in the original water sample (Burnison and Leppard 1983).

Discussion

The sequential ethanol precipitation procedure (Fig. 1), applied to lacustrine fibrils that were isolated and concentrated by physical separation techniques, provides a fibril fraction with the following characteristics in approximately 60% yield: (1) absence of any major category of colloidal impurity detectable by TEM, (2) relative freedom from fibrils of atypical morphology, (3) relative freedom from a class of small granules typically associated with lacustrine fibrils and with some other kinds of polyanionic fibrillar colloids found in nature, (4) freedom from derivatization reactions, and (5) freedom from an undesirable exposure to caustic reagents.

Burnison and Leppard (1983) showed that the complex cationic stain, ruthenium red, when applied to a lacustrine colloid fraction would give rise to a precipitate extremely enriched in colloidal organic fibrils. This technique for obtaining a fibril-rich sample has a serious disadvantage, however, in that it creates a fibril derivative that precludes many chemical analyses of fibrils for their binding properties.

The physically isolated "colloidal" fraction (Burnison and Leppard 1983) had some complex biological activities, including at least one enzymatic activity that could confuse assays for fibril binding characteristics (G. G. Leppard and B. K. Burnison, unpubl. data). For this reason, we chose to deactivate fibril fractions at the first stage in final purification not requiring freedom from denaturation. The heating step of choice did not alter fibril morphology. The addition of sodium acetate to the enzyme-deactivated sample (Fig. 1) was important because without it the ethanol precipitation was very slow and the precipitate was difficult to collect. An understanding of the mode and nature of fibril aggregation may become amenable through the use of colloidal fibril fractions, and this in turn may lead to an increased understanding of their adhesion and sedimentation properties in the aquatic environment.

Finally, we noted that the granular impurities illustrated in Fig. 2C and 2E had a similarity in size to ribosomes (and, as a possible consequence, a potential source of phosphate). Assays done according to Burnison (1978) indicate, however, that they do not contain nucleic acid. One idea that we wish to pursue is that the granules may represent a condensed form of the polyanions that make up a major constituent of the fibrils.

Acknowledgments

We sincerely thank Donna Nuttley and Dina Paolini for their technical assistance. We also thank the following scientists from the Department of Biology, McMaster University, Hamilton, Ont., for their assistance with electron microscope facilities: Dr J. Lott, Mr E. Spitzer, and Mrs B. Singh.

References

BURNISON, B. K. 1978. High molecular weight polysaccharides isolated from lake water. Verh. Int. Ver. Limnol. 20: 353–355.

BURNISON, B. K., AND G. G. LEPPARD. 1983. Isolation of colloidal fibrils from lake water by physical separation techniques. Can. J. Fish. Aquat. Sci. 40: 373–381.

GHOSH, K., AND M. SCHNITZER. 1980. Macromolecular structures of humic substances. Soil Sci. 129: 266–276.

JEANLOZ, R. W. 1970. Mucopolysaccharides of higher animals, p. 589–625. *In* W. Pigman and D. Horton [ed.] The carbohydrates — chemistry and biochemistry. 2nd ed. Vol. IIB. Academic Press, New York, NY.

LEPPARD, G. G., AND B. K. BURNISON. 1983. Bioavailability, trace element associations with colloids and an emerging interest in colloidal organic fibrils, p. 105–122. *In* G. G. Leppard [ed.] Trace element speciation in surface waters and its ecological implications. Plenum Publishing Corp., New York, NY.

LEPPARD, G. G., A. MASSALSKI, AND D. R. S. LEAN. 1977. Electron-opaque microscopic fibrils in lakes: their demonstration, their biological derivation and their potential significance in the redistribution of cations. Protoplasma 92: 289–309.

WHISTLER, R. L., AND J. L. SANNELLA. 1965. Fractional precipitation with ethanol-purification of hemicelluloses, p. 34–36. *In* R. L. Whistler [ed.] Methods in carbohydrate chemistry. Vol. 5. General polysaccharides. Academic Press, New York, NY.

Incubation of the Eggs of Atlantic Salmon, *Salmo salar*, at Low Temperatures

Tor G. Heggberget

Directorate for Wildlife and Freshwater Fish, Sverresgt. 1. N-7000 Trondheim, Norway

Jeff C. Wallace

Institute of Fisheries, University of Tromsø, P.O. Box 3083 Guleng N-9001 Tromsø, Norway

Heggberget, T. G., and J. C. Wallace. 1984. Incubation of the eggs of Atlantic salmon, *Salmo salar*, at low temperatures. Can. J. Fish. Aquat. Sci. 41: 389–391.

Eggs of Atlantic salmon (*Salmo salar*) from the River Alta in northern Norway were subjected to three experimental temperature regimes during prehatching incubation. Two of these were intended to simulate possible temperature situations in the river after hydroelectrical development of its upper reaches. The third temperature regime was that of the natural river. The results indicated that hydroelectrical development of the Alta may lead to an earlier hatch of the salmon embryos in the river. Incubation time, and perhaps also a "trigger" such as rising temperature, may be more important than the heat sum (degree-days) of the incubation period in determining the exact timing of the hatch.

Des œufs de saumons atlantique (*Salmo salar*) de la rivière Alta, dans le nord de la Norvège, ont été soumis à trois régimes thermiques expérimentaux au cours de l'incubation précédant la mue. Deux de ces régimes devaient simuler des conditions possibles dans la rivière après un développement hydroélectrique en amont. Le troisième était le régime thermique naturel de la rivière. Les résultats ont démontré que le développement hydroélectrique de l'Alta a été la cause d'une éclosion hâtive des embryons de saumon dans la rivière. La durée de l'incubation et possiblement un mécanisme de déclenchement, tel qu'une température ascendante, peut avoir une plus grande importance que la somme calorifique (degrés-jours) de la période d'incubation dans la détermination du moment exact de l'éclosion.

Received July 22, 1983
Accepted November 23, 1983

Reçu le 22 juillet 1983
Accepté le 23 novembre 1983

The temperature of water from storage basings seldom approaches freezing point, even at Arctic latitudes. Deep reservoir water, being most dense at 4°C, is insulated from subzero air temperatures by the colder, less dense water layer below the surface ice. In contrast, river water, which in winter in the Arctic consists of a relatively shallow layer running under ice, is usually cooled to a temperature very close to freezing. It is under such conditions that river organisms or (more usually) their eggs overwinter.

Many Arctic river systems are now being altered to make reservoirs for the production of hydroelectricity, a development that results in the lower reaches of rivers being supplied not from smaller streams but from large reservoirs. One of the many effects of such alterations is a change in the temperature of the river water. The reservoir can act as a "heat sink," giving higher river temperatures in winter and lower temperatures in summer.

Atlantic salmon (*Salmo salar*) in Norwegian streams normally spawn from September to December and hatch from April to June. Change of the winter temperature of a salmon river can, therefore, be expected to affect the velocity of incubation of salmon eggs and possibly the ability of salmon to reproduce successfully in the river.

A model describing the dependence of the incubation period of salmon eggs on water temperature has been proposed by Crisp (1981). However, the available experimental data on egg incubation in salmonid species have been obtained from experiments conducted at temperatures no lower than 2.4°C (Embody 1934; Peterson et al. 1977; Alderdice and Velsen 1978; Carrick 1979; Gunnes 1979). Predictions of incubation times at water temperatures below this are, therefore, based on extrapolations from reported data and not from observations (Crisp 1981).

Our aim was to observe the effects of three low-temperature regimes on the incubation periods of Atlantic salmon eggs from the River Alta, northern Norway (70°N, 23°E), the upper reaches of which are being developed for hydroelectrical generation.

Material and Methods

Equipment designed for experiments in running water at controlled temperatures as low as 0.1°C was constructed at the University of Tromsø. The open aquarium system was constructed to simulate river water temperatures and changes in these due to hydroelectrical development in Arctic regions. The water temperatures could be accurately controlled to as low as 0.1°C.

The planned dam on the River Alta will have two outlets to the power station, one close to the bottom (−78 m) and the other 10 m from the water surface. The temperature regimes for the experiment were therefore chosen to simulate the following possible situations after development. (A) River temperatures

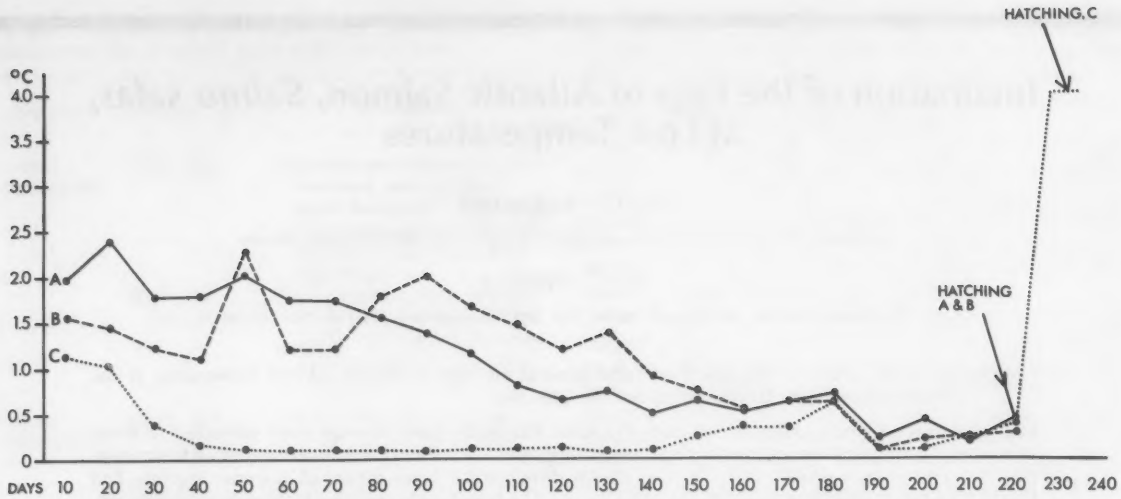


FIG. 1. Temperature regimes experienced by groups of eggs, plotted as the mean temperatures for each 10 d of the investigation.

when water is supplied from the bottom outlet from the dam. The mean water temperature during 214 d was 1.31°C, with variations from 2.9 to 0.2°C. (B) River temperatures when water is supplied mostly from the high outlet, with occasional changes to the bottom outlet causing temporary temperature rises. The mean water temperature during 214 d was 1.10°C, with variations from 4.0 to 0.1°C. (C) River temperatures in the natural situation. The mean temperature during 232 d was 0.65°C and the range from 4.0 to 0.1°C.

The experiment was begun on October 27, 1982, and concluded on June 15, 1983. The eggs used were from one pair of Atlantic salmon taken from the River Alta just before spawning. They were separated into groups of about 2000 eggs, referred to as groups A, B, and C according to the temperature to which they were subjected.

Results

Despite a heat sum difference of about 15% (40 degree-days) between groups A and B, hatching occurred simultaneously in the two groups (Table 1). The mean temperature of the group A eggs was about 0.5° higher than that of the group B eggs during the early incubation, while during the middle period of the experiment the reverse was the case. During the last part of the incubation the temperature was about the same in the two groups (Fig. 1).

In group C, which experienced the lowest water temperatures, 50% hatching occurred about 14 d later than in the other groups. In group C the temperature was raised rather drastically, from 0.4°C at the end of May to 4.0°C in June; this probably accelerated development, and it might have triggered hatching. However, some eggs in group C hatched as early as May 28, after about 90 degree-days. Egg mortality was insignificant in all groups.

Discussion

It is generally known that the number of degree-days required by fish eggs during prehatching incubation is lower at low water temperatures than at higher temperatures, and the results presented here are in accordance with this knowledge. According to the model proposed by Crisp (1981) for estimating times

TABLE 1. Mean temperatures, times to 50% hatch, and heat sums to 50% hatch for the three groups of eggs.

Egg group	Mean temperature (°C)	Time to 50% hatch (d)	Heat sum to 50% hatch (degree-days)
A	1.31	214	280
B	1.10	214	239.5
C	0.65	232	150.6

to hatching at the temperatures used here, the hatching of groups A and B should have occurred at, respectively, 191 and 198 d. However, both groups hatched at 214 d. The slight discrepancy between the predicted and the observed results may have one or several explanations.

The model may not hold for temperatures as low as those used here. As has been mentioned, the model is based on observations made at higher temperatures, predictions for low temperatures being made by extrapolation.

The genetic variation between strains of Atlantic salmon (Ryman and Ståhl 1981; Thorpe and Mitchell 1981) may also contribute to differences in incubation interval among stocks. The data upon which Crisp's model is based have been obtained from salmon stocks from more southern, and presumably warmer, rivers than the Alta. Alta salmon may be "cold adapted" with respect to their egg incubation period.

It is interesting that hatching occurred simultaneously in groups A and B and that some eggs in group C also hatched at the same time. At the time of hatching, water temperature was rising. It had been increased by about 0.7° for all groups the previous day. This may have triggered the hatching process. However, the embryos in the three groups had experienced temperature regimes that resulted in different heat sums at the time of hatching, which points to a conclusion reached by several authors that hatching is not necessarily a precise indicator of the embryo's developmental stage but is, partly at least, independent of it (Gray 1928; Hayes and Armstrong 1942; Hayes et al. 1953; Smith 1957). Certainly time and perhaps also rising temperature, rather than heat sums alone, apparently have

determined the point at which our eggs in groups A and B hatched.

The point of 50% hatch for group C eggs, exposed at a mean temperature of 0.65°C, was 232 d and a heat sum of 150.8 degree-days. This is roughly in accordance with the model.

The conclusion from this experiment is that if hydroelectrical development of the River Alta results in the kind of temperature regimes investigated, then the data of hatching of salmon eggs in the river may be advanced by at least 2 wk. The significance of early hatching and alevin survival will depend on factors not yet contemplated.

Acknowledgments

Thanks are due to Arne Kolbeinshavn, Georg Silvertsen, and Dagfinn Aasjord for surveillance of the equipment during the experiment. The study was financed by the Norwegian Hydroelectrical Board.

References

ALDERDICE, D. F., AND F. P. J. VELSEN. 1978. Relation between temperature and incubation time for eggs of Chinook salmon (*Oncorhynchus tshawytscha*). J. Fish. Res. Board Can. 35: 69–75.

CARRICK, T. R. 1979. The effect of acid water on the hatching of salmonid eggs. J. Fish Biol. 14: 165–172.

CRISP, D. T. 1981. A desk study of the relationship between temperature and hatching time for eggs of five species of salmonid fishes. Freshw. Biol. 11: 361–368.

EMBODY, G. C. 1934. Relation of temperature to the incubation periods of eggs of four species of trout. Trans. Am. Fish. Soc. 64: 281–292.

GRAY, J. 1928. The growth of fish. III. The effects of temperature on the development of eggs of *Salmo fario*. Br. Exp. Biol. 6: 110–124.

GUNNES, K. 1979. Survival and development of Atlantic salmon eggs and fry at three different temperatures. Aquaculture 16: 211–218.

HAYES, F. R., AND F. H. ARMSTRONG. 1942. Physical changes in the constituent parts of developing salmon eggs. Can. J. Res. 20: 99–114.

HAYES, F. R., D. PELLUET, AND E. GORHAM. 1953. Some effects of temperature on the embryonic development of the salmon (*Salmo salar*). Can. J. Zool. 31: 42–51.

PETERSON, R. H., H. C. E. SPINNEY, AND A. SREDHARAN. 1977. Development of Atlantic salmon (*Salmo salar*) eggs and alevins under varied temperature regimes. J. Fish. Res. Board Can. 34: 31–43.

RYMAN, N. AND G. STÅHL. 1981. Genetic perspectives of the identification and conservation of Scandinavian stocks of fish. Can. J. Fish. Aquat. Sci. 38: 1562–1575.

SMITH, S. 1957. Early development and hatching, p. 323–359. *In* M. E. Brown [ed.] The physiology of fishes. I. Academic Press, New York, NY.

THORPE, J. E., AND K. A. MITCHELL. 1981. Stocks of Atlantic salmon (*Salmo salar*) in Britain and Ireland: discreteness and current management. Can. J. Fish. Aquat. Sci. 38: 1576–1590.

BOOK REVIEWS/COMPTES RENDUS

Research on Fish and Wildlife Habitat. *William T. Mason Jr. (Technical Editor), U.S. Environmental Protection Agency, Washington, DC (EPA600/8-82-022). 1982. 248 p. Prices not indicated.*

The volume is a monograph of contributed papers by members of U.S. government agencies (Environmental Protection Agency, U.S. Fish and Wildlife, U.S. Department of Agriculture Forest Service), university, and industry presenting various methodologies that have been employed in environmental and data management and environmental impact statements. Most papers in the monograph relate their particular topic to the National Environmental Policy Act (NEPA) of 1969, which was the launching pad for the development of Environmental Impact Statements of the 1970s. The title and the foreword suggest a technically specific emphasis that is not there. The foreword gives the purpose of the volume as being the Office of Research and Development (ORD)'s "... effort to take stock of scientific advances in fish and wildlife habitat since the inception of the Agency and to gauge what progress has been made and what remains to be accomplished." Michael Zagata, author of one of the contributions and the closing paper, observed that most of the authors discussed a particular classification system, inventory methodology, or assessment and planning framework. The reader should not expect to find a technical delineation of the cutting edge of research on topics relating to fish and wildlife. Given a change in the title and a more accurate description in the foreword that emphasizes developments and progress in methodology for information management, environmental management guidelines, approaches to problem solving, management decision making, and data management, I think the monograph would be much stronger and directed to a more relevant audience of government agencies, legal administrative bodies, industrial environmental coordinators, consultants, and others in environmental management.

Some indication of how these papers were put together (invited presentation, workshops, written critique) would have assisted in providing a better framework for the reader to evaluate the papers in context. Nonetheless, the monograph is extremely useful in offering the benefits of anectodal experience based on various approaches to environmental inventory and assessment. In this regard, the monograph is also useful to those in resource management and those interested in developing a better knowledge of Environmental Impact Assessment techniques. Each paper provides good references from the primary literature, government, and consultant reports making it a useful source document for interested readers.

Mount's paper placed this monograph of the 1970–80 period in best perspective, with his observation that the fifties were concerned with domestic sewage, the sixties with methods development and testing, and the seventies with rapid improvement in methods and data generation. His prognosis for the eighties is a period of rapid progress in prediction and more efficient use of resources because of the foundation developed in the previous decade.

Taken together, the monograph's papers also provide a worthwhile perspective (except for the title) of the development of our understanding of environmental systems to 1980 and the shaping of national and regional policies in the United States over the decade.

G. A. VIGERS

E.V.S. Consultants Ltd.
195 Pemberton Avenue
North Vancouver, B.C. V7P 2R4 (R494)

Theory and Management of Tropical Fisheries. *Edited by D. Pauly and G.I. Murphy. ICLARM Conference Proceedings 9. 1982. 360 p. Available from International Scholarly Book Services Inc., P.O. Box 1632, Beaverton, OR 97075, USA. $28.50 (U.S.) softbound, $32.50 (U.S.) hardbound.*

This volume is the proceedings of the ICLARM/CSIRO Workshop of the same title held at Cronulla, Australia, 12–21 January, 1981. In the context of applications to tropical fisheries management, the workshop's objectives were (1) to review models presently used or proposed for use for stock assessment in the tropics, (2) to define the data requirements of various stock assessment and management methods, (3) to review current research on stock assessment in tropical waters, and (4) to identify the major constraints for stock assessment and management in tropical waters and plan means to overcome them.

There are two reasons why this volume is of interest to students of the population dynamics of fishes in temperate waters as well as the few who pursue such studies in the tropics. The first reason is that the models applied to tropical fish resources are usually the same as, or closely related to, those applied in temperate waters, although the data base for parameter estimation is weaker. The six modeling papers of the volume are of general applicability. The second reason is the distilled knowledge and wisdom of the distinguished contributors and participants, which is evident in the review papers and workshop report. The 14 participants had ample opportunity to thoroughly debate the issues during these 10 days together.

Among the modeling papers, your attention is drawn to contributions by D. Pauly, G. P. Kirkwood, P. A. Larkin, and W. Gazey, J. Majkowski, and K. J. Sainsbury. These papers reviewed, respectively, models of growth, mortality, and recruitment of fishes together with related questions of parameter estimation, the usefulness of differential equation models of fish population abundance including the multispecies Schaeffer model, the use of computer simulation models in tropical fisheries management, the usefulness of sensitivity analysis in

multispecies populations modeling, and the adequacy of general ecological models based on cybernetics or ecological niches as a basis for developing models of the dynamics of exploited fish communities.

R. Jones contributed a wide-ranging comparative study of fish ecosystems and related fisheries yields. Also of interest was a study of coral reef fish communities by P. F. Sale and a comparative study of fish yields from tropical ecosystems by G. G. Marten and J. J. Polovina.

Papers by J. A. Gulland and J. C. Marr put the methodological and ecological papers in the perspective of practical fishery management in the tropics.

The organization of the volume is good, with indices of geography, cited names, and taxonomy. Unfortunately, the soft cover copy provided for review was poorly bound so that several pages fell out.

In conclusion, the organizers and the workshop chairman, Dr Larkin, succeeded in producing a stimulating and useful volume. As always with such workshops, more problems were identified than solved, but this does not limit the value of the book to fisheries scientists.

W. G. DOUBLEDAY

Atlantic Fisheries Service
Department of Fisheries and Oceans
Ottawa, Ont. K1A 0E6

(R516)

Stratégies d'échantillonnage en écologie. *Edité par S. Frontier. Collection "Ecologie" No 17. Masson, Paris et Les Presses de l'Université Laval, Québec, Qué. 1982. 494 p.*

Un ouvrage sur l'échantillonnage destiné aux écologistes est intéressant dans la mesure où il se situe entre les généralités connues de tous et la théorie mathématique poussée susceptible de provoquer de nombreuses indigestions. Plusieurs chapitres de ce livre se situent bien entre ces deux extrêmes. Cet ouvrage comprend 13 chapitres écrits par 20 auteurs français et québécois qui tentent de dégager les principes généraux devant présider à l'échantillonnage et au traitement des données. Toutefois, de l'aveu même de l'éditeur, l'ouvrage ne se veut pas un traité sur l'échantillonnage ni une mise au point exhaustive de l'état actuel des réflexions sur le sujet, mais plutôt un recueil d'idées sur l'échantillonage.

Le livre se divise en deux parties inégales. La première comprend 4 chapitres (270 pages) assez généraux, où sont exposés les choix et les contraintes de l'échantillonnage en écologie (Frontier), les techniques de sondage (Scherrer), l'échantillonnage et le traitement des données (P. Legendre et L. Legendre) et le traitement des signaux quantitatifs et leurs implications pour l'échantillonnage (Laurec). Dans cette première partie, les chapitres de Scherrer et de Legendre et Legendre retiennent particulièrement l'attention. Le traitement des techniques de sondage est fort complet. Scherrer y présente sept plans d'échantillonnage, la théorie s'y rapportant, leurs conditions d'application, les contraintes et les inconvénients qu'ils suscitent et les pièges à éviter dans leur utilisation. C'est un chapitre écrit clairement, bien étoffé d'exemples et qui colle aux problèmes concrets auxquels doivent faire face les écologistes. Le chapitre suivant est de même facture, il complète bien le chapitre précédent. On y discute de la précision des données, des méthodes d'analyse et d'interprétation des structures de groupement et d'ordination, les conditions régissant leur emploi, et on y présente aussi l'analyse des séries écologiques et les principales méthodes permettant d'identifier une périodicité dans les données (corrélogrammes, périodogrammes, analyse spectrale). Ces deux chapitres méritent à eux seuls qu'on achète le livre.

La deuxième partie, comprenant les 9 autres chapitres (185 pages), se veut une présentation de cas concrets dans différents domaines. Ces présentations sont fort inégales et laissent une impression de décousu due aux différentes approches utilisées; tantôt on se limite à la présentation de solutions adoptées au cours d'études particulières, tantôt on examine les problèmes associés à un type d'analyse ou à une technique de récolte.

Outre les chapitres 5 et 13 qui portent respectivement sur l'échantillonnage en milieu terrestre et sur l'échantillonnage en fonction d'une modélisation, les chapitres de cette section tirent leurs exemples du milieu aquatique : l'échantillonnage du phytoplancton lacustre, d'un peuplement de poissons en migration, du benthos marin et les problèmes liés à l'échantillonnage en continu en océanographie et à la diversité spécifique.

Trois chapitres de cette section doivent être soulignés. R. Arfi, F. Blanc et D. Calmet présentent un examen intéressant des méthodes d'analyse utilisées au cours de leurs travaux en milieu pélagique au large de Marseille, travaux qui font appel aux approches temporelles eulérienne et lagrangienne. On y retrouve plusieurs applications de l'analyse en composantes principales et du traitement par analyse spectrale. Le chapitre portant sur l'échantillonnage en continu en océanographie, présenté par F. Ibanez, constitue aussi une section intéressante et concise des problèmes associés à ce type d'échantillonnage en mer; l'auteur y examine le traitement des données au cours de l'échantillonnage et les techniques de comparaison de stations et de groupes de stations. Enfin, le chapitre de S. Frontier sur l'échantillonnage de la diversité spécifique constitue également une revue éclairée des divers indices disponibles, de leur utilité, de leurs limites et des contraintes que leur utilisation impose aux stratégies de récolte des données.

Le livre est complété par une imposante liste bibliographique : à peu près de la moitié des quelque 500 titres mentionnés sont postérieurs à 1975. Il constitue donc une bonne introduction à la littérature portant sur l'échantillonnage.

Par ailleurs, sur le plan éditorial, il faut noter une impression qui n'est pas toujours très nette, des omissions dans la liste des références, des erreurs typographiques et d'autres erreurs associées aux citations d'auteurs dans le texte.

En bref, malgré quelques lacunes, cet ouvrage contient de solides chapitres sur les stratégies d'échantillonnage, une liste bibliographique à jour. Il devrait donc s'avérer utile aux étudiants des cycles supérieurs et aux écologistes confrontés à des problèmes particuliers sur le terrain. Ils y trouveront des conseils sur les meilleures stratégies à adopter pour la récolte et le traitement de leurs données.

E. Bourget

GIROQ
Département de biologie
Faculté des sciences et de génie
Université Laval
Ste-Foy, Qué. G1K 7P4

(R476)

BOOKS RECEIVED/LIVRES REÇUS

November/novembre 1983

Oceanography. The present and future. *Edited by P. G. Brewer. Springer-Verlag, New York, NY. 1983. xii + 392 p. $39.80 (U.S.).* The book comprises the proceedings of a symposium held at the Woods Hole Oceanographic Institution, Sept. 29–Oct. 2, 1980, on the 50th anniversary of its founding. The 22 contributors address the current status and future trends in their area of ocean science. [R525]

Global Fisheries. Perspectives for the 1980s. *Edited by B. J. Rothschild. Springer-Verlag, New York, NY. 1983. xii + 289 p. $34.80 (U.S.).* A collection of 13 perspectives on the state of fishery policy and management provide a framework for considering fishery policy under the extended jurisdiction regime of the 1980s. [R526]

Air–Sea Exchange of Gases and Particles. *Edited by P. S. Liss and W. G. N. Slinn. D. Reidel Publishing Company, Hingham MA 02043, USA. 1983. xiii + 56 p. $69.50 (U.S.).* This book arises from a NATO-sponsored Advanced Study Institute held in July 1982. The eight chapters are the written versions of the lectures presented, whose objective is to give the reader a basic understanding of how material exchange takes place at the air–sea interface. [R527]

Guide to the Early Stages of Marine Fishes Occurring in the Western North Atlantic Ocean, Cape Hatteras to the Southern Scotian Shelf. *M. P. Fahay. J. Northw. Atl. Fish. Sci. 4: 424 p. 1983. $20 (Canada) paper, $30 (Canada) cloth (available from Executive Secretary, Northwest Atlantic Fisheries Organization, Bedford Institute of Oceanography, P.O. Box 638, Dartmouth, N.S. B2Y 3Y9).* Guide contains descriptions of eggs and larvae of fishes likely to be collected in plankton and neuston samples on continental shelf and adjacent oceanic waters. [R528]

***Theory and Management of Tropical Fisheries.** *ICLARM Conference Proceedings 9. Edited by O. Pauly and G. I. Murphy. 1982. 360 p. $6.50 (U.S.).* The multiauthored book comprises proceedings in an ICLARM/CSIRO workshop whose objectives were to (1) review models currently used or proposed for stock assessment in the tropics, (2) define data requirements of stock assessment and management methods, (3) review current research on stock assessment in tropical waters, and (4) identify major constraints on assessment and management in the tropics and how they can be overcome. [R529]

**Available from ICLARM, MCC P.O. Box 1501, Makati, Metro Manila, Philippines.*

***Preliminary Bibliography of Rice–Fish Culture.** *R. M. Temprosa and Z. H. Shehadeh. ICLARM Bibliographies 1. 1980. 20 p. $4.50 (U.S.).* [R530]

***An Annotated Bibliography of Slipmouths (Pisces: Leiognathidae).** *S. Pauly and S. Wade-Pauly. ICLARM Bibliographies 2. 1981. 62 p. $7 (U.S.).* [R531]

***A Bibliography of Important Tilapias (Pisces: Cichlidae) for Aquaculture.** *P. Schoenen. ICLARM Bibliographies 3. 1922. 336 p. $32.50. (U.S.)* [R532]

***Hanging Culture of the Green Mussel (*Mytilus smaragdinus* Chemitz) in Thailand.** *P. Chonchuenchob, K. Chalayondeja, and K. Muttarasin. ICLARM Translations 1. 1979. 14 p. $2 (U.S.).* [R533]

***Fecundity, Egg Weight, and Ocyte Development in Tilapias (Cichlidae, Teleostei).** *H. M. Peters. ICLARM Translations 2. Edited by D. Pauly. 1983. 28 p. $5.35 (U.S.) (translated from German).* [R534]

***The Economics of the Milkfish Fry and Fingerling Industry of the Philippines.** *I. R. Smith. ICLARM Tech. Rep. 1. 1981. 147 p. $21.50 (U.S.).* This report is the first of several dealing with the economics of the milkfish *Chanos chanos* industry. [R535]

***The Economics of Catfish Farming in Central Thailand.** *T. Panayotou, S. Wattanutchariya, S. Isvilanonda, and R. Tokrisna. ICLARM Tech. Rep. 4. 1982. 60 p. $10 (U.S.)* Study reports results of a recall survey of 41 catfish farms in 1979 to ascertain why production had been declining since 1974, despite high and rising market prices for catfish. [R536]

***The ICLARM-CLSU Integrated Animal–Fish Farming Project: Final Report.** *K. D. Hopkins and E. M. Cruz. ICLARM Tech. Rep. 5. 1982. 96 p. $7.75 (U.S.) surface, $14.85 (U.S.) airmail.* Report presents data collected on pig–fish, duck–fish, and chicken–fish systems over a 3-yr period. [R537]

***Production and Marketing of Milkfish in Taiwan: An Economic Analysis.** *C.-H. Lee. ICLARM Tech. Rep. 6. 1983. 41 p. $6.30 (U.S.) surface, $9.50 (U.S.) airmail.* Economic aspects of the Taiwanese milkfish resource system and its major subsystems of fry procurement, baitfish rearing, market-size rearing, and marketing are considered in the report. [R538]

***Small-Scale Fisheries of San Miguel Bay, Philippines: Biology and Stock Assessment.** *ICLARM Tech. Rep. 7. Edited by D. Pauly and A. N. Mines. 1983. 124 p. $16 (U.S.).* A multidisciplinary research project on biological, economic, and sociological aspects of the San Miguel fisheries was conducted from 1979 to 1981 to obtain a factual base from which options for managing the Bay's fishery could be derived. This report presents objectives and methodology of the biological portion of the project and serves as background to seven other papers. [R539]

***Small-Scale Fisheries of San Miguel Bay, Philippines: Occupational and Geographic Mobility.** *C. Barley. ICLARM Tech. Rep. 10. 1982. 57 p. $11.50 (U.S.).* The report analyzes existing and potential sources of alternative employment for fishermen and their families in the San Miguel Bay area and effects these alternatives have or might have on reducing levels of fishing effort. [R540]

***A Japanese Fishing Joint Venture: Worker Experience and National Development in the Solomon Islands.** *S. K. Meltzoff and E. S. LiPuma. ICLARM Tech. Rep. 12. 1983. 63 p. $6.55 (U.S.) surface, $10.90 (U.S.) airmail.* What motivates islanders to take part in fisheries development schemes and how they react to the conflicts between village and fishing port life are documented in this penetrating report. [R541]

***Small Boat Design.** *ICLARM Conference Proceedings No. 1. 79 p. Edited by J. M. Reinhart. 1979. $12 (U.S.).* Proceedings of the ICLARM Conference on Small Boat Design, Noumeau, New Caledonia. [R542]

***Caribbean Coral Reef Fishery Resources.** *J. L. Munro. ICLARM Studies and Reviews 7. 1983. 276 p. $16 (U.S.) surface, $33 (U.S.) airmail (paper); $19.50 (U.S.) surface, $37 (U.S.) airmail (cloth).* The information in the report was first published in mimeograph form by the University of the West Indies. It is based on field work conducted from 1969 to 1973 in Jamaica and presents the first systematic application of the theory of fishing and of modern stock assessment methods to a tropical fishery and the first ever to a coral reef fishery. [R543]

***Applied Genetics of Tilapias.** *G. W. Wohlfarth and G. Hulata. ICLARM Studies and Reviews 6. 1983. 26 p. $5.25. (U.S.).* The authors take a broad view of applied genetics and summarize much of the information on the biology and distribution of tilapias that the culturist must appreciate before assessing an approach to genetic manipulation. [R544]

***Review of Breeding and Propagation Techniques for Grey Mullet, *Mugil cephalus* L.** *C. E. Nash and Z. H. Shehadeh. ICLARM Studies and Reviews No. 2. 1980. 87 p. $11.50 (U.S.).* Prepared as a part of ICLARM's program on the controlled breeding and mass propagation of food fishes, the review comprises a compendium of most of the available biological and engineering knowledge relevant to breeding and mass propagation of mugilid species, especially the grey mullet. [R545]

***A Research Framework for Traditional Fisheries.** *I. R. Smith. ICLARM Studies and Reviews No. 2. 1979. 45 p. $6.50 (U.S.).* The monograph's aim is to identify those areas of traditional fisheries research that have the greatest potential for solving problems facing traditional fishermen and their communities. Following an overview that examines the goals and potentially conflicting objectives of development planning, problems of traditional fisheries are categorized as either suppositional or empirical. [R546]

***Theory and Management of Tropical Multispecies Stocks. A Review, with Emphasis on the Southeast Asian Demersal Fisheries.** *D. Pauly. ICLARM Studies and Reviews No. 1. 1979. 35 p. $6.50 (U.S.).* The paper's four parts cover the marine fisheries of Southeast Asia, mathematical models used to monitor these fisheries and predict yields, and the possible new approaches in the study and management of the region's fisheries. [R547]

Proceedings of 1981 Workshop on Care and Maintenance of Natural History Collections. *Syllogeus 44. Edited by D. J. Faber. 1983. 196 p. (available by mail from the National Museum of Natural Sciences, Ottawa, Ont. K1A 0M8).* Thirty papers on collection, preparation, storage, and documentation of specimens, plus miscellaneous considerations. [R548]

Man-Made Carbon Dioxide and Climatic Change. A Review of Scientific Problems. *P. S. Liss and A. J. Crane. Geo Books, Norwich, England. 1983. vii + 127 p. $7 (U.S.) paper, $17 (U.S.) cloth.* Global behavior of anthropogenic CO_2 and climatic consequences of increased atmospheric CO_2 are reviewed in the first two sections of the book. A concluding section addresses questions related to the CO_2 problem of special concern to energy industries. [R549]

Methods de determination de l'âge des poissons etudiés dans le cadre du Programme sur le poisson de fond de la Station de biologie du Pacifique. *D. E. Chilton and R. J. Beamish. Publ. spéc. can. sci. halieut. aquat. 60. 1983. 102 p. $7 (Canada), $8.40 (other countries).* Manual describes methods and equipment used to estimate ages of groundfish species studied by the Pacific Biological Station. English edition also available. [R550]

Corals of the World. *E. M. Wood. T.F.H. Publications, Neptune, NJ. 1983. 256 p. $29.95 (U.S.).* The professional and amateur are treated to 290 color photographs, 158 black and white photographs, species descriptions, and distribution maps of reef-building corals of the Atlantic, Pacific, and Indian oceans. [R551]

CORRECTIONS TO RECENT PUBLICATIONS
CORRECTIONS SUR RÉCENTS PUBLICATIONS

VOLUME 40, No. 9 — note by R. K. Misra and I-H. Ni: *Distinguishing beaked redfishes (deepwater redfish,* Sebastes mentella, *and Labrador redfish,* S. fasciatus*) by discriminant analysis (with covariance) and multivariate analysis of covariance.*

PAGES 1507–1511: The common name "Labrador redfish" in the title and text of this note should not be construed as acceptance of this name by the authors. On the contrary, Ni (1982, Can. J. Fish. Aquat. Sci. 39: 1678) has argued that the distribution of *Sebastes fasciatus* renders the epithet "Labrador" inappropriate. The names used in the note are those recommended by the American Fisheries Society (1980, Special Publication No. 12) and were an editorial addition for which we apologize.

VOLUME 39, No. 8 — note by W. Y. B. Chang: *A statistical method for evaluating the reproducibility of age determination.*

PAGE 1208: The expression

$$\left(\frac{(\Sigma X_{ij} - X_j)^2}{R(R-1)}\right)^{1/2} \Big/ X_j$$

is incorrect. The correct difference between the average percent error (APE) and the coefficient of variation (V) is

$$\left(\sqrt{\bar{A}} - \frac{\sqrt{R}}{\sqrt{R-1}}\sqrt{\bar{A}}\right) \Big/ X_j$$

where $\sqrt{\bar{A}}$ is the average of $\sqrt{(X_{ij} - X_j)^2}$ and $\bar{A}$ is the average of $(X_{ij} - X_j)^2$.

ANNOUNCEMENTS/AVIS

1984 International Conference on Biology of Pacific Salmon

The 1984 International Conference on Biology of Pacific Salmon will be held September 4–12, 1984. Its purpose is to bring together the widest possible spectrum of international participants to discuss recent findings on the biology of Pacific salmon. Enhancement activities directed at Pacific salmon have accelerated tremendously in the entire North Pacific and are also underway in New Zealand, Chile, France, eastern United States, and the Great Lakes area. Thus, it is hoped that the conference will disseminate new knowledge, experience, and technology on the biology of these valuable species.

Conference registration will begin on September 4, 1984, at the Empress Hotel, Victoria, B.C. The presentations will begin on the morning of September 5 and continue until noon on September 7. Participants will then be given an opportunity to visit research facilities and hatcheries until the evening of September 9. The formal presentations will resume on the morning of September 10 at the Harrison Hot Springs Hotel, Agassiz, B.C., and conclude at noon on September 12.

Subjects to be discussed at this conference may include but are not restricted to the following:

- Ocean carrying capacity
- Migration behavior (coastal, freshwater)
- Predation
- Physiology
- Reproduction
- Pathology
- Enhancement strategies

The deadline for submission of abstracts is April 1, 1984. Decisions on acceptance of or rejection of papers will be July 1, 1984.

Further information on hotels and tours will be given later.

F. K. Sandercock, Ph.D.
Organizing Chairman

Conférence internationale de 1984 sur la biologie des saumons du Pacifique

La Conférence internationale de 1984 sur la biologie des saumons du Pacifique aura lieu du 4 au 12 septembre 1984. Son objectif est de réunir un éventail aussi large que possible de participants internationaux qui y analyseront les récentes découvertes touchant les saumons du Pacifique. Les activités de revalorisation de ces poissons se sont considérablement intensifiées dans tout le Pacifique nord, et il se fait également des travaux en Nouvelle-Zélande, au Chili, en France, dans l'est des États-Unis et dans la région des Grands Lacs. On espère donc que la Conférence contribuera à diffuser information, expérience et technologie relative à la biologie de ces espèces de valeur.

L'inscription débutera le 4 septembre 1984 à l'hôtel Empress, à Victoria (C.-B.). La présentation des travaux débutera dans la matinée du 5 septembre et se poursuivra jusqu'à midi, le 7 septembre. Les participants auront alors l'occasion de visiter les installations de recherche et de pisciculture jusque dans la soirée du 9 septembre. Les présentations formelles recommenceront dans la matinée du 10 septembre à l-hôtel Harrison Hot Springs, à Agassiz (C.-B.), pour se terminer à midi, le 12 septembre.

Seront discutés à la Conférence les sujets suivants (sans toutefois qu'ils y soient limités):

- Capacité de transport des océans
- Comportement migratoire (près de la côte, en eau douce)
- Prédation
- Physiologie
- Reproduction
- Pathologie
- Stratégie de revalorisation

Les résumés des communications devront être soumis avant le 1 avril 1984. L'acceptation ou le rejet d'articles se fera le 1 juillet 1984.

Les détails relatifs aux hôtels et excursions vous seront transmis plus tard.

F. K. Sandercock, Ph.D.
Président du programme

COMING NEXT MONTH/À PARAÎTRE LE MOIS PROCHAIN

Articles

Estimating stock composition in mixed stock fisheries using morphometric, meristic, and electrophoretic characteristics **D. A. Fournier, T. D. Beacham, B. E. Riddell, and C. A. Busack**

Periodicity of egg laying and egg age distributions in planktonic Cladocera **A. J. Tessier**

An evaluation of morphometrics and meristics for stock separation of Pacific herring (*Clupea harengus pallasi*) **H. J. Meng and M. Stocker**

Environmental factors influencing the production of an antibacterial metabolite from a marine dinoflagellate, *Prorocentrum minimum* **C. G. Trick, R. J. Andersen, and P. J. Harrison**

Growth and survival of developing steelhead trout (*Salmo gairdneri*) continuously or intermittently exposed to copper **W. K. Seim, L. R. Curtis, S. W. Glenn, and G. A. Chapman**

Empirical prediction of crustacean zooplankton biomass and profundal macrobenthos biomass in lakes **J. M. Hanson and R. H. Peters**

Optimal versus unregulated industry behavior in a Beverton–Holt multicohort fishery model **K. Stollery**

Geochemical pathways and biological uptake of radium in small Canadian Shield lakes **R. H. Hesslein and E. Slavicek**

Analysis of echo counting data: a model **R. Kieser and T. J. Mulligan**

Changes in the selection of microhabitat by juvenile Atlantic salmon (*Salmo salar*) at the summer–autumn transition in a small river **D. M. Rimmer, U. Paim, and R. L. Saunders**

Inter- and intra-population variation in the fecundity of chinook salmon (*Oncorhynchus tshawytscha*) and its relevance to life history theory **M. C. Healey and W. R. Heard**

Population dynamics of western Arctic bowhead whales (*Balaena mysticetus*) **J. M. Breiwick, L. L. Eberhardt, and H. W. Braham**

Prediction of chlorophyll *a* concentrations in Florida lakes: importance of aquatic macrophytes **D. E. Canfield, Jr., J. V. Shireman, D. E. Colle, W. T. Haller, C. E. Watkins, II, and M. J. Maceina**

Small-scale covariability in the abundance of fish larvae and their prey **L. Fortier and W. C. Leggett**

A gastric evacuation model for young yellow perch, *Perca flavescens* **E. L. Mills, R. C. Ready, M. Jahncke, C. R. Hanger, and C. Trowbridge**

Notes

Dual cannulation of free-swimming Atlantic salmon, *Salmo salar* **D. J. Nichols and M. Weisbart**

Abundance and distribution of humpback whales (*Megaptera novaeangliae*) in West Greenland waters **J. S. Perkins, K. C. Balcomb, III, G. N. Nichols, Jr., and M. DeAvilla**

Crab response to prey density can result in density-dependent mortality of clams **E. G. Boulding and T. K. Hay**

Accumulation and metabolism of tri-*n*-butyltin cation by a green algae, *Ankistrodesmus falcatus* **R. J. Maguire, P. T. S. Wong, and J. S. Rhamey**

Opportunistic cyclopoid predation on fish larvae **J. H. Hartig and D. J. Jude**

Use of a self-cleaning, in-line filter to continuously monitor phytoplankton nutrient uptake rates **J. S. Parslow, P. J. Harrison, and P. A. Thompson**

Canadian Journal of Fisheries and Aquatic Sciences

Journal canadien des sciences halieutiques et aquatiques

Volume 41, No. 2, February 1984 — Volume 41, nº 2, février 1984

Articles

Utilization of phytoplankton by zooplankton during the spring bloom in a Nova Scotia inlet R. J. Conover and P. Mayzaud **232–244**

Distribution of digestive enzymes in zooplankton during the spring bloom in a Nova Scotia inlet P. Mayzaud and R. J. Conover **245–252**

An integration of forest and lake fertilization: transport and transformations of fertilizer elements C. J. Perrin, K. S. Shortreed, and J. G. Stockner **253–262**

Deposition of fine and coarse sand in an open-work gravel bed P. A. Carling **263–270**

Resource management biology for the edible kelp *Cymathere triplicata* W. G. Rowland **271–277**

Recent colonization of a major salmon-producing lake in British Columbia by Pacific lamprey (*Lampetra tridentata*) S. P. Farlinger and R. J. Beamish **278–285**

Distributions of ferrous iron and sulfide in an anoxic hypolimnion R. B. Cook **286–293**

Ichthyoplankton associated with a warm core ring off the Scotian Shelf J. S. Wroblewski and J. Cheney **294–303**

Development of larvae of the saffron cod, *Eleginus gracilis*, with comments on the identification of gadid larvae in Pacific and arctic waters contiguous to Canada and Alaska J. R. Dunn and B. M. Vinter **304–318**

Spawning site water chemistry and lake trout (*Salvelinus namaycush*) sac fry survival during spring snowmelt J. M. Gunn and W. Keller **319–329**

Divergent structure in fish taxocenes of north temperate streams R. Mahon **330–350**

Contribution of particulate phosphorus (>250 μm) to the total phosphorus pool in lake water E. E. Prepas and J. Vickery **351–363**

Behavioral response of blacknose dace (*Rhinichthys atratulus*) to varying densities of predatory creek chub (*Semotilus atromaculatus*) D. F. Fraser and E. E. Emmons **364–370**

Characterization of protease from the myxosporean salmon parasite, *Henneguya salminicola* E. Bilinski, N. P. Boyce, R. E. E. Jonas, and M. D. Peters **371–376**

Notes

Fyke net catches as indices of the abundance of brook trout, *Salvelinus fontinalis*, and Atlantic salmon, *Salmo salar* P. M. Ryan **377–380**

An improved flow-through respirometer for aquatic macroinvertebrate bioenergetic research F. J. Wrona and R. W. Davies **380–385**

Ethanol fractionation of lacustrine colloidal fibrils B. K. Burnison and G. G. Leppard **385–388**

Incubation of the eggs of Atlantic salmon, *Salmo salar*, at low temperatures T. G. Heggberget and J. C. Wallace **389–391**

Book reviews/Comptes rendus

Research on fish and wildlife habitat (W. T. Mason Jr.) G. A. Vigers **392**

Theory and management of tropical fisheries (D. Pauly and G. I. Murphy [ed.]) W. G. Doubleday **392**

Stratégies d'échantillonnage en écologie (S. Frontier [ed.]) E. Bourget **393**

Books received/Livres reçus **394–395**

Corrections to recent publications/Corrections sur récents publications **396**

Announcements/Avis **397**

Coming next month/À paraître le mois prochain **398**

CJFSDX41(2) 231–398 (1984)
ISSN 0706-652X
© Minister of Supply and Services Canada 1984
Ministre des Approvisionnements et Services Canada 1984